Wehle, Duff Henry Strong

THE BREEDING BIOLOGY OF THE PUFFINS: TUFTED PUFFIN (LUNDA CIRRHATA), HORNED PUFFIN (FRATERCULA CORNICULATA), COMMON PUFFIN (F. ARCTICA), AND RHINOCEROS AUKLET (CERORHINCA MONOCERATA)

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A

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THE BREEDING BIOLOGY OF THE PUFFINS:

TUFTED PUFFIN (LUNDA CIRRHATA),

HORNED PUFFIN (FRATERCULA CORNICULATA),

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ABSTRACT

The natural histories of Tufted and Horned puffins (Lunda cirrhata and Fratercula corniculata) were studied during the summer on Buldir Island, Alaska, in 1975 and on Ugaiushak Island, Alaska, in 1976 and 1977. Data from these and other recent studies have been presented and compared with that available for Common Puffins (F. arctica) and Rhinoceros Auklets (Cerorhinca monocerata)--actually a misnamed puffin--to provide synthesis of the natural history of the world's four species of puffins. Different aspects of puffin natural history show varying degrees of interspecific variability. Preferences of nesting habitats and patterns of colony settlement are similar for Tufted and Common puffins, while the length of incubation, brooding, and nestling periods are similar for Tufted Puffins and Rhinoceros Auklets. Sexual and social behaviors are similar for the congeneric Horned and Common puffins. All species have two to four vocalizations in common. Nest building, nest-site tenacity, nest-site cohabitation, territoriality, egg replacement, and the participation by both sexes in incubation and feeding of young are characteristic of all puffins. For all colony-years reported, the average range of breeding success rates for puffins are 50-60% for laying success, 75-90% for hatching success, and 53-82% for fledging success. Puffins exhibit considerable seasonal and geographic inter-and intraspecific variation in their foraging habitats. Fish is the most important prey for all adult puffins, although squid, polychaetes, and crustaceans are con-

sumed to varying degrees by each species. Sand lance (Ammodytes spp.) is the most common prey fed to all puffin nestlings. Nestling growth rates are highest in Tufted and Horned puffins when sand lance are supplemented with Capelin (Mallotus villosus) and in Common Puffins when sand lance are supplemented with sprats (Sprattus sprattus).

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INTRODUCTION

In terms of both the number of species and of individual birds, Alaska's seabird colonies are among the most spectacular in the world. Between 40 and 50 million seabirds of at least 35 species breed in Alaska (Sowls et al. 1978; D.D. Gibson, pers. comm.).

Alcids (Family Alcidae) comprise at least 65% of Alaska's breeding seabird population, and approximately 20% of these are puffins: Tufted Puffin (Lunda cirrhata), Horned Puffin (Fratercula corniculata), and Rhinoceros Auklet (Cerorhinca monocerata)--actually a misnamed puffin (Storer 1945). Tufted and Horned puffins in Alaska comprise roughly half of the estimated world population of these two species, and Rhinoceros Auklets comprise approximately one-third of their world population.

Potential and existing conflicts between the conservation of marine birds and uses of other resources in Alaska and elsewhere in northern North America have been presented in Bartonek and Nettleship (1979). Paramount among these conflicts is the development of petrochemical resources in these areas. King and Sanger (1979) reported that among 176 species of birds using the marine habitats in Washington State, British Columbia, and Alaska, the three Pacific puffins ranked among the highest in vulnerability to oil pollution. If the consequences of petrochemical exploitation are to be predicted and safeguards established against potential problems, we must have an adequate knowledge of the ecology of those species which may be affected (McKnight and Knoder 1979). This dissertation is intended

to provide, at least in part, the ecological information on puffin biology needed as the first step of this management process.

This dissertation presents a comparative analysis of selected aspects of the natural history of the three Pacific puffins and their Atlantic relative, the Common Puffin (F. arctica). Until recently, the natural history of the Tufted and Horned puffins was the least well known of the four puffin species, with most information coming from numerous general accounts (e.g., Barlow 1894, Dawson 1913, Willett 1915, Bent 1919, Dement'ev and Gladkov 1951, Kozlova 1957, Dickerman 1960, Thompson 1967, and others) and a few specific studies (Swartz 1966, Cody 1973, Sealy 1973b, Frazer 1975). The status of our knowledge of these two species has changed dramatically in the last few years, primarily as the result of studies conducted by the U.S. Bureau of Land Management/National Oceanic and Atmospheric Administration Outer Continental Shelf Environmental Assessment Program (OCSEAP).

My fieldwork in 1975 was conducted from 17 May to 5 September on Buldir Island, AK, (52° 21'N, 175° 56'E), the westernmost member of the Rat Island group of the Aleutian Islands (Fig. 1). The island's physiogeography, flora, and fauna have been described by Sekora (1973) and Wehle (1976).

In 1976 and 1977, I conducted fieldwork as a part of OCSEAP studies on Ugaiushak Island, AK, (56°47'N, 156°41'W) located approximately 13 km southeast of the Alaska Peninsula and 126 km northeast of the coastal village of Chignik (Fig. 1). Descriptions of the island's physiogeography, flora, and fauna have been presented in OSCEAP

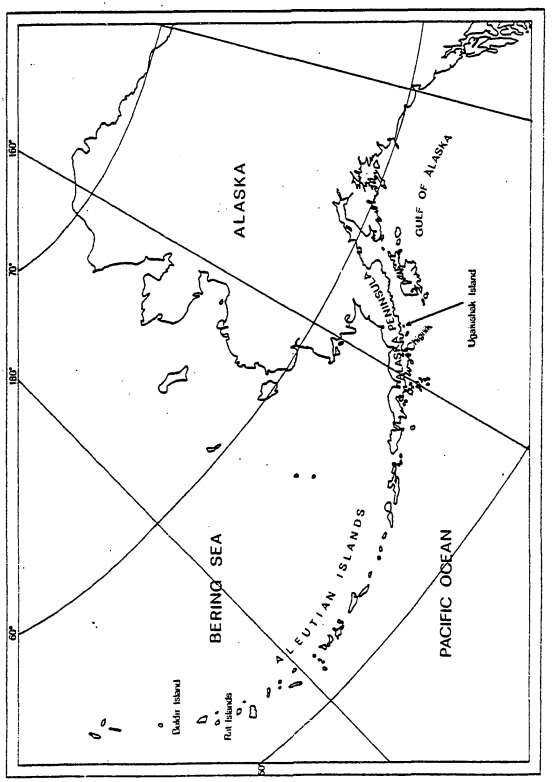


Figure 1. Location of Buldir Island and Ugaushak Island, Alaska.

reports (Wehle et al. 1977, Wehle 1978). Fieldwork was conducted from 24 May to 2 September 1976 and from 23 April to 29 August 1977.

In addition to fieldwork conducted in Alaska, during the spring of 1977 and 1978 and during the summer of 1979, I visited several Common Puffin colonies in Scotland and the state of Maine to observe puffin behavior.

CHAPTER I: COMPARATIVE BREEDING BIOLOGY AND FEEDING ECOLOGY OF TUFTED AND HORNED PUFFINS, LUNDA CIRRHATA AND FRATERCULA CORNICULATA

In this chapter, I present and compare data on the breeding biology and feeding ecology of Tufted and Horned puffins obtained from my own field investigations conducted during the summers of 1975-1977, from other OCSEAP studies, and from a number of other independent studies. The purpose of this chapter is to present new data relating to the natural history of these species and to summarize available information concerning the ecology of these species and thus provide a foundation of knowledge upon which future management decisions may be based.

NESTING HABITAT

The majority of the Tufted Puffins on Buldir and Ugaiushak islands nested in earthen burrows. The habitat in which these burrows were located differed between the islands, but all nests were situated that birds could quickly take-off and land. On Buldir Island, most burrows were located on steep seaslopes which afforded the greatest soil depth of any available habitat. On Ugaiushak Island, the greatest soil depths (up to 1.5m) were along the tops of the sea cliffs surrounding the island, and it was here that the majority of birds nested; seaslopes were covered with only a few centimeters of topsoil. A few Tufted Puffins on Buldir Island nested along the cliff-edges

where they dug their burrows into the shallow layer of topsoil at the exposed rock/soil interface. On Ugaiushak Island, burrows in this habitat extended inland up to 5 m from the cliff-edge.

Most of the remaining Tufted Puffins on both islands nested in rock crevices in vegetated talus slopes. Nest-sites in this habitat were usually a combination of earthen burrows dug through the topsoil and rock crevices lying underneath.

Throughout their range, most Tufted Puffins nest in earthen burrows, usually along the cliff-edge (Willett 1915, Preble and McAtee 1923, Dement'ev and Gladkov 1951, Rausch 1958, Cody 1973, Dick et al. 1976, Hatch et al. 1979) but also commonly on seaslopes (Drent and Guiguet 1961, Amaral 1977, Hatch et al. 1979). Colonies on cliff-edges usually have a higher burrow density than those on seaslopes, and Amaral (1977) found a positive correlation between the angle of slope and burrow density. Although common in some areas, fewer Tufted Puffins nest in rock crevices of talus slopes and beach boulders or in combination burrow/crevices in seaslopes or vegetated talus slopes (Drent and Guiguet 1961, Sealy 1973b). Density in these rock crevice habitats, appears to be lower than in the earthen burrow habitats. Tufted Puffins also nest in cracks and crevices located in a cliff-face, when these are available (Drent and Guiguet 1961, Swartz 1966, Sealy 1973b, Hunt 1977), but nest density is usually low because of the scarcity of such sites.

In addition to these common habitats, Tufted Puffins occasionally nest elsewhere: on the open ground under bushes (Bent 1919); in sandy burrows on an estuarine islet subject to tidal flooding (Gill and

Sanger 1979); and in a shipwreck (Hatch et al. 1979).

The primary nesting habitat used by Horned Puffins on both Buldir and Ugaiushak islands was rock crevices located in talus slopes or among beach boulders. The greatest densities of Horned Puffins were found in sections of bare talus, but they were also common in surrounding vegetated talus areas where they used combined burrow/crevices. Although Tufted Puffins also used these vegetated talus areas, Horned Puffins usually predominated. Horned Puffins nested extensively in cracks and crevices in cliff-faces on both islands; however, the availability of such nest-sites was limited. A few Horned Puffins nested in earthen burrows dug into seaslopes or into the banks of inland creeks and hillsides on Buldir Island but not on Ugaiushak Island.

While Horned Puffins on Buldir Island frequently nested 300 m or more above sea level, Tufted Puffins seldom nested at elevations greater than 150-200 m. On Ugaiushak Island, both species nested from sea level to the highest elevation on the island (approximately 170 m).

Throughout their range, most Horned Puffins nest in rock crevices in talus slopes and among beach boulders (Willett 1915, Heath 1915, Dement'ev and Gladkov 1951, Kenyon and Brooks 1960, Swartz 1966, Sealy 1973b, Amaral 1977). In this habitat the density of Horned Puffins is usually high, with several pairs frequently using the same entrance to a network of chambers beneath the surface. In most cases, this habitat is shared with at least one other species.

The next most preferred habitat appears to be cracks and crevices located in cliff-faces (Willett 1915, Dement'ev and Gladkov 1951,

Sealy 1973b, Hunt 1977). Densities of birds using this habitat are low as a result of its unavailability. Although cliff-face habitat seems preferred, more Horned Puffins probably nest in combined burrow/crevices in areas of vegetated talus. Densities here tend to be less than in bare talus or beach boulder areas, but greater than in areas where birds nest in cracks and crevices in cliff-faces.

In a few areas (Middle Punuk Island, AK [Thompson 1967]; Chamisso Island, AK [Grinnell 1900, Degange and Sowls 1978]; Alyumka Island in the Anaydr Estuary, [Kozlova 1957]; and possibly on Kodiak Island, AK, [Bent 1919]) Horned Puffins nest in earthen burrows which they excavate. On Chamisso Island, the burrows are located on cliff-tops within several meters of the cliff-edge and on steep seaslopes.

Horned Puffins appear less inclined than Tufted Puffins to nest in atypical habitat, though they may nest in sea caves, presumably in cracks in the rock (J. L. Trapp, pers. comm.; R. H. Day, pers. comm.).

On Buldir Island Horned Puffins nested at higher elevations than Tufted Puffins. The situation is reversed on East Amatuli Island, AK, where Amaral (1977) did not find Horned Puffins nesting above 100 m, while Tufted Puffins nested from 12 m to the island's summit (469 m). Similarly, throughout the Aleutians, Gabrielson and Lincoln (1959) reported Horned Puffins nesting from the surf to the crest of the islands. On Forrester Island, AK, Willett (1915) never observed them nesting more than 30 m above sea level.

THE PRE-EGG STAGE

Arrival and Settlement

Arrival and settlement of Tufted and Horned Puffins at the breeding colonies involves four events: 1) first arrival, 2) first land-coming, 3) establishment of continuous occupancy, and 4) initiation of egg-laying.

First arrival of birds generally consists of a few scattered individuals appearing offshore, followed within a couple of days by the population arriving en masse. There is a direct correlation between the time of arrival and latitude, with Tufted Puffins arriving 2 to 3 mo and Horned Puffins 1 to 2 mo later at the northern than southern limits of their ranges (Appendix I). At the same colony, each species generally arrives within the same 1- to 2-week period each year.

Once present offshore, Tufted and Horned Puffins exhibit differences in their patterns of colony settlement (Appendix II). The interval between first arrival and first land-coming is usually 1 to 2 weeks for Tufted Puffins and less than 1 week for Horned Puffins.

First landing of Horned Puffins generally coincides with establishment of continuous occupancy, after which birds are consistently present in high numbers at or in the vicinity of the colony. For Tufted Puffins, however, continuous occupancy usually follows first land-coming by several weeks. During this period, Tufted Puffins regularly exhibit a quasi-cyclical (Nettleship 1972) pattern of attendance at or in the vicinity of the colony, with birds present in high

numbers for several days followed by their almost total absence for an equivalent period while they are at sea. On Ugaiushak Island in 1977, Tufted Puffins were present on or near the colony for 4 to 5 days before going to sea for an equal period of time. The birds underwent four such cycles before establishing continuous occupancy. The length of individual cycles varies between colonies and possibly also between years at the same colony. Stejneger (1885) reported birds present for 1 day followed by 2 days at sea, and Amaral (1977) observed numbers varying in a 3 to 5 day cyclic pattern. Similar periodic fluctuations in numbers have been reported by Kozlova (1957) and Frazer (1975), but these authors did not indicate the length of the cycles observed.

Cyclic patterns of attendance at breeding colonies have not been observed for Horned Puffins (Swartz 1966, Amaral, 1977, this study). Amaral (1977) and Wilson (1977) incorrectly cite me (Wehle 1976) as having observed this phenomenon in Horned Puffins; however, the observations referred to occurred prior to the arrival of the population en masse.

The presence and absence of cyclic patterns of attendance during the pre-egg stage of Tufted and Horned puffins is probably related to their feeding habits. I seldom observed Tufted Puffins but regularly observed Horned Puffins feeding nearshore during the pre-egg stage. During periodic absences of Tufted Puffins from the colony, these birds apparently traveled to distant foraging areas to feed.

Once continuous occupancy has been established, egg-laying generally follows within 1 week for Tufted Puffins and within 2-3 weeks for Horned Puffins (Appendix II).

Throughout their ranges the total length of the pre-egg stage averages about 3.5 weeks for Tufted Puffins and 3 weeks for Horned Puffins. However, the length of the pre-egg stage increases with latitude for Tufted Puffins but is relatively stable for Horned Puffins (Appendix II).

Behavior

During each field season, I observed the behavior of Tufted and Horned puffins. Observations of birds on the water were made from either cliff-top vantage points or from a boat. On land, I established canvas blinds in each of the major colonies of both species. Blinds erected after the arrival of the birds in 1975 resulted in heavy desertion by birds in the immediate vicinity of the blinds. Consequently, all blinds were erected in following years prior to the birds' establishment of continuous occupancy.

In Tufted Puffin colonies, I marked each burrow with numbered stakes to facilitate recognition and recording of visitations and affinities of individual birds to particular burrows. Such markings did not appear to have any adverse effect on the birds' normal behavior. In Horned Puffin colonies, observations were limited to birds present on the exposed, outer rocks of the talus slopes and beach boulder areas.

Since trapping and marking of birds caused nest desertion, I recognized individual birds in study areas by morphological, behavioral, or vocal peculiarities. Behavioral postures and displays illus-

trated in the following discussion are based on photographs. Previous descriptions of these behaviors in the literature are limited (i.e., Stejneger 1885, Frazer 1975, Amaral 1977).

Sexual Behavior

Tufted and Horned puffin sexes are essentially monomorphic, although males are generally slightly larger than females. Both species undergo an incomplete prenuptial molt in late winter or early spring (Bent 1919, Dement'ev and Gladkov 1951, Kozlova 1957). This molt provides them with adornments (see Kozlova 1957, Amaral 1977) apparently important for sexual and social behaviors during the breeding season, as some adornments begin to lose their brilliance as the breeding season progresses and all adornments are lost during the complete postnuptial molt.

Whether mate selection occurs at sea prior to the return of the birds to the breeding colonies or in the nearshore waters during the pre-egg stage is unknown; however, courtship begins soon after the birds' arrival.

Courtship ceremony leading to copulation.--The courtship ceremony of Tufted and Horned puffins is very similar. Copulation usually takes place in nearshore waters of the breeding colony amidst a flock of rafting birds. Horned Puffins appear to be more social on the water than Tufted Puffins, forming tighter rafts and associating more in pairs. As courtship begins, the male lowers the back of his head to

his shoulders and holds his bill in a horizontal plane parallel to the rest of the body (Figure 2). The bill is then alternately raised to a near vertical position and then lowered back toward the horizontal, with the mandibles opening on the up-stroke and closing on the down-stroke as if the bird was repeatedly tossing and catching a pea in mid-air with the tip of his mandibles. In Tufted Puffins, the bill is lowered completely back to the horizontal on the downstroke, but in Horned Puffins the bill is lowered only about half-way down. The frequency of this head-jerking is slightly faster in Horned than Tufted Puffins. It is not known whether vocalization accompanies the mandibular movement. When the mandibles are open, the brightly colored linings of the buccal cavity are exposed and the pink rosettes at the commissural points are expanded. Soon after this display begins, the male follows the female at a distance of several meters. If the female is interested in copulation, she swims rapidly ahead of the male and assumes a crouched posture low to the water. As the male approaches closer, his head-jerking becomes more exaggerated and quickened in pace. If the female still remains interested, she slows her swimming speed, and when the male is within approximately a meter of her, he flaps his wings, rises out of the water, and alights on top of her. The female then sinks so that only her head remains above the water. The male flaps his wings throughout coition and may or may not continue to head-jerk. Sometimes the male pecks the female sharply on the head with his bill. Coition usually ends by the female diving out from beneath the male and surfacing a meter or so away. The sequence is completed when one and usually both birds wing-flap (see below).

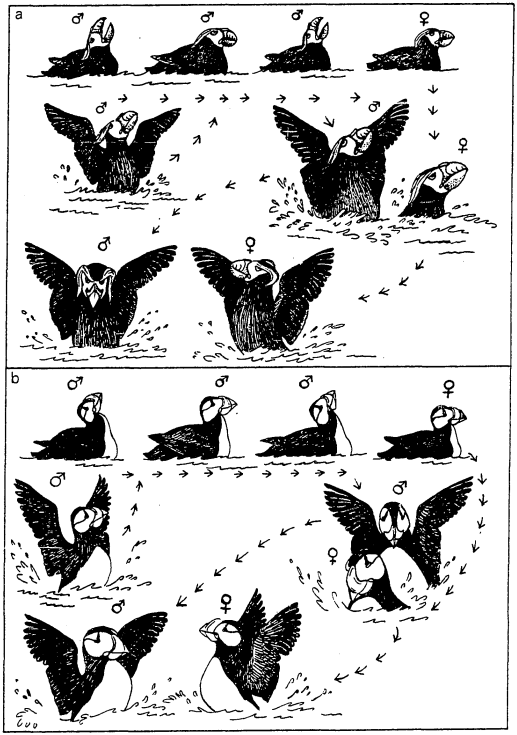


Figure 2. Illustration of Tufted (a) and Horned (b) puffin courtship ceremony leading to copulation. (Illustration by Rachelle Hunt)

Interspersed with the behaviors described above are several other behaviors which show no pattern in the frequency of courtship ceremonies in which they occur, in the time at which they occur during the ceremony, or in the sex of the bird displaying the behavior. These behaviors in both species include bill-dipping, wing-flapping, bill-gaping, and billing; and in Horned Puffins, mutual head-jerking (see below).

The courtship ceremony frequently attracts the attention of nearby birds in the raft. Sometimes these spectators attempt to "bill" (see below) with one or the other principals and sometimes several birds adopt the head-jerking display and form an entourage behind the female. In most cases when another bird becomes involved in the ceremony, successful coition is not achieved.

The vigor with which the male head-jerks and opens and closes his mandibles appears to be important in determining if coition will follow. Particularly early in the pre-egg stage, a male will follow a female, jerking his head up and down but not opening and closing his mandibles. Successful coition usually does not follow on these occasions.

If a particular female does not respond positively to a male, he may divert his attentions to a nearby bird of either sex (as deduced from previous behavior of the spectators). In one instance, I observed a rejected male Tufted Puffin mount and copulate with the large, globular float of a Bull Kelp (Nerocystis luetkean).

Billing.--Courtship and maintenance of the pair bond in Tufted and Horned Puffins is based largely on billing. Billing occurs on the water especially during the pre-egg stage and on land throughout the breeding season. Either member of a pair may initiate billing.

Usually the initiating bird assumes a low profile, holding its head slightly downward, and moving it slowly from side to side, in a pendulum-like repetitive motion. If the other bird appears responsive, the first bird begins to gently nuzzle the throat and breast feathers of the other. It then repeatedly brings its bill up, under the lower mandible of the other bird until it is in a position in which billing can occur.

Billing consists of two birds facing each other with the side of the bill of one bird pressed against the opposite side of the bill of the other bird. (Figure 3a). The two birds then move their heads from side to side with their bills separating from each other momentarily before being slapped together again. When the bills make contact, a sound is produced similar to that heard when the broadsides of two plastic rulers are hit against each other. The postures of the two birds vary. On water, both birds assume a low profile with their necks outstretched. On land, one bird usually stands erect with its nape and breast feathers fluffed out and its head lowered. The other bird crouches low to the ground with its feathers sleeked and its head raised slightly upward. On both land and water, one, both, or neither bird may have its tail raised above its wing-tips. Bouts may range in length from only a few seconds to several minutes and be repeated several times per hour.

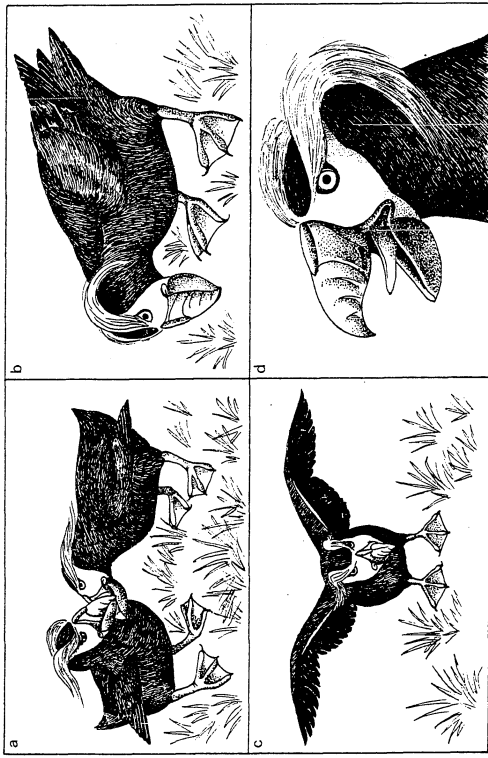


Figure 3. Illustration of Tufted Puffin billing (a), bowed-head Display (b), landing display (c), and bill-gaping (d). (Illustration by Rachelle Hunt)

Throughout the breeding season, billing of a pair on land frequently follows the landing of one bird next to its mate on the colony, or occurs 1) prior to the entry of both birds into the nest-site, 2) after an aggressive action by one member of the pair towards a third bird, 3) after head-jerking (Horned Puffin), or 4) after a bowed-head display (Tufted Puffin). In all of these situations, the apparent function of billing is to maintain the pair-bond.

I have also observed billing or its precursory movements in several situations involving the feeding of young. In one instance, a Horned Puffin delivering the first meal to its newly hatched chick entered the nest-site, dropped the fish, lowered its head and moved it several times from side to side while uttering a faint "errr" sound. This movement, without the accompanying vocalization, is similar to that of one adult inviting another to bill. At the conclusion of this behavior, the chick walked over to and immediately ate the food. Also, nestling Tufted and Horned puffin chicks raised in captivity regularly attempted to bill with my fingers when I offered them food. These observations suggest that billing or its precursory movements may have been evolutionarily related to feeding.

Neighboring birds commonly participate in the billing ceremony. Members of the original pair may bill with any or all of the outsiders. Usually the larger bird of the pair, presumably the male, erects his nape feathers and, in the case of Tufted Puffins, his plumes, and bill-gapes (see below) at the intruders. If this behavior is not sufficient to drive the intruding neighbors off, a fight usually ensues and billing is temporarily terminated.

Head-jerking.--Both Tufted and Horned puffins head-jerk as a part of the courtship ceremony, but I have only seen Horned Puffins head-jerk in other contexts. Head-jerking in these instances is less exaggerated than during the courtship ceremony, with the head usually raised less than 60° above the horizontal and the mandibles seldom opened. The contexts in which this display occurs vary. On water, a number of birds may head-jerk simultaneously, apparently not at any other particular bird. Sometimes spectators of a courting pair will follow the pair and head-jerk. In rare cases, both members of the courting pair will head-jerk at each other.

On land, head-jerking may occur in birds standing or sitting alone, in pairs when one or both birds may be doing it, and in small groups when one, several, or all the birds are involved in this display. Frequently, head-jerking between two individuals leads to billing.

Bowed-head Display.--I have observed the bowed-head display only in Tufted Puffins. The body is held low and horizontal to the ground with the head tilted downward so that the tip of the bill nearly touches the substrate (Figure 3b). The head is then swung slowly from side to side. In some cases, this side to side movement is accompanied by rhythmic convulsions of the body. Apparently, some form of vocalization accompanies this movement (Z. Eppley, pers. comm.). This display is most common at the entrance to a burrow. The bird usually faces inside, although in some instances the bird may face away from the burrow or stand on top of the burrow with its bill-tip in the

entrance. In most cases the mate is nearby, and the display has the effect of drawing this bird to the burrow. Once there, both birds may bill, followed by the first bird resuming the bowed-head display as it walks into the burrow. If the second bird does not follow, the first bird emerges, continues displaying, and again walks into the burrow. This behavior is repeated until both birds have entered the burrow or until the first bird stops displaying.

The bowed-head posture apparently creates a strong drive to bill. During the early pre-egg stage in 1977, I placed a stuffed male Tufted Puffin in the bowed-head posture at the entrance to a burrow that had been visited regularly by a pair of Tufted Puffins. When one member of this pair returned, it immediately ran up to the stuffed bird, lowered its head, and attempted to bill. This bird continued trying to bill with the stuffed bird for about 2 min before it flew off. The other member of the pair then landed about 2 m away from its burrow and was joined almost immediately by its mate. Both birds then billed. Afterward, one began the bowed-head display but did not receive much further attention from its mate. A third bird appeared from a nearby burrow and walked over to the stuffed bird and tried to bill. After 1 min, this bird walked over to the displaying member of the pair and billed with it. All birds then flushed.

Social Behavior

Behaviors discussed below include those other than sexual behaviors, which directly relate to potential or actual encounters between

individuals. Territoriality or "territorial behavior" is also discussed in this section.

Fly-bys.--Commonly during the pre-egg stage, but continuing throughout the breeding season, Tufted and Horned puffins make repeated circular flights over the breeding colony and adjacent water before settling in nearshore rafts or landing on the colony (Stejneger 1885, Frazer 1975, Wehle 1976, Amaral 1977). These "fly-bys" may involve only a few individuals or may consist of virtually the entire population of the colony. The function of this behavior is unclear but may involve social stimulation and/or predator avoidance.

Landing Display.--Both Tufted and Horned puffins use a display immediately after landing on the colony. Once landed, the body is held low to the ground with the wings held up above the back and outstretched distally from the humerus (Figure 3c). The head may also be outstretched in line with the body or may be bent downward varying degrees. This position is held several seconds. There appears to be a positive correlation between the duration of the display and the number of birds in the immediate vicinity of the landing and a negative correlation between the duration of the display and the distance to the nearest bird. At the conclusion of the display, the bird usually takes several exaggerated steps in this posture before slowly closing the wings and assuming a normal posture.

Although this display is in the repertoire of both species, Horned

Puffins do not always use it, and when they do, its duration is usually shorter than in the Tufted Puffins.

Bill-gaping.--Bill-gaping is the most important threat display exhibited by Tufted and Horned puffins. The bird stands erect with neck stretched upwards and bill facing the recipient of the threat. The neck and head feathers are ruffled, and in Tufted Puffins, the plumes are raised (Figure 3d). The mandibles are held wide apart, exposing the brightly-colored linings of the mouth, and the tongue may or may not protrude. Bill-gaping is superficially similar to yawning; however, in yawning, the neck feathers are not ruffled and the tongue seldom, if ever, is protruded.

The duration of the threat presumably varies in proportion to the seriousness of intent. In general, however, it does not exceed 5 sec. Frequently at the end of the display, when the bill is closed, there is a rhythmic mandibular movement. I am uncertain whether any vocalization accompanies bill-gaping.

Bill-gaping usually occurs in response to an intrusion of another bird in one's territory (see territoriality); before, during, and after a fight; by unwilling partners during the courtship ceremony; and when a third bird attempts to join in the billing of a pair.

In 1977, I placed a stuffed bird in the bill-gaping posture at the entrance to a burrow used by a pair of Tufted Puffins. When the owners of the burrow returned, both wing-flapped, shook their heads several times, and one bill-gaped, facing away from the stuffed bird. A bird from a neighboring burrow then landed about 2 m from the

stuffed bird and bill-gaped several times directly at the mount. One of the members of the original pair then bill-gaped at the stuffed bird, at first with the mandibles held widely apart and then with the mandibles closed to within about 1 cm of each other. This posture was retained for about 2 min before all birds flushed from the colony.

Fighting.--Fighting is usually the result of one bird trespassing on another's territory (see territoriality) or the intrusion of a third bird while a pair is billing. The bird intruded upon generally warns the intruding bird by bill-gaping, feather ruffling, and, in Tufted Puffins, plume erection. When fighting occurs, the wings are usually held outstretched and are flapped periodically, presumably for balance. The feet are used to push the other bird away as well as to inflict damage with the sharp claws.

A bird is victorious when it has the other's bill within its own and its feet on the other's breast, thereby completely dominating the other bird. Fights may go on for several minutes, frequently ending by both birds tumbling down the slope, talus, or off the cliff-edge. Sometimes the fight will continue on the sea below. The victor usually returns to the colony immediately.

A deep gutteral sound is the only specific vocalization accompanying the fight. When fighting involves one member of a pair, it is usually the larger of the two, presumably the male, that partakes in the battle. I have never seen more than two birds involved in a fight.

Territoriality.--Territorial behavior is most keen during the pre-egg stage, and gradually lessens in importance throughout the rest of the breeding season. Tufted Puffins defend the area in the immediate vicinity of their burrow. The defended area usually includes the burrow entrance, the approach path to the burrow, and a specific area that is used for landing and as a resting site when the birds are on colony. The latter area may consist of a grass hummock, a mound of earth, or a projecting rock surface near the burrow entrance. Usually the territory has a radius of less than 0.5 m from the burrow entrance. In areas where burrow density is low a stretch of "no man's land" may exist between territories. Most birds tend to remain within the boundaries of their territory.

I never saw Horned Puffins defend or fight at the entrance to their nest-sites. I did, however, hear fighting deep within the crevices and I suspect that this species defends only the nest itself.

Body-Care Behavior

The functions of the three behaviors discussed below are related to the maintenance of normal body functions.

Head-dipping.--Both Tufted and Horned puffins head-dip when swimming. The behavior consists simply of the bird lowering its head into the water so that it is submerged to just above the eyes. I have not been able to discern any particular context in which this behavior occurs, having observed it by birds alone, in pairs, amidst small and

large rafts, during the courtship ceremony, and before and after billing. It may be that this behavior is a comfort movement rather than a social signal, perhaps serving to keep the eyes moist.

Wing-flapping.--Wing-flapping, like head-dipping, occurs in a variety of contexts on land and water in both Tufted and Horned puffins. This behavior consists of the bird assuming an erect posture, fluffing out the feathers of the entire body, and beating its wings back and forth several times. The wings are held at an angle during beating so that the white-edged tertials are directed slightly forward. Tufted Puffins usually beat their wings 2 to 4 times, and Horned Puffins 7 to 10 times. At the completion of the wing-beating, the head is usually shaken several times.

Wing-flapping probably serves as a comfort movement to replenish the supply of insulative trapped air in the feathers. However, it does appear to be contagious--when one bird wing-flaps one or several birds nearby also wing-flap.

Preening.--Tufted and Horned puffins preen both on the water and on land. The broad side of the bill is repeatedly rubbed on the uropygial gland, and the secretion smeared over the feathers. The primaries and retrices are then drawn singly through the tip of the bill. Preening serves the function of waterproofing, feather maintenance, and the removal of ectoparasites.

Vocalizations

Reports in the literature of the vocalizations of Tufted and Horned puffins range from describing these birds as almost silent (Bent 1919, Gabrielson and Lincoln 1959, Amaral 1977) to ascribing to them a great number of quarrelsome growl-like sounds (Dement'ev and Gladkov 1951, Kozlova 1957). I recognized four vocalizations, and each was superficially similar between Tufted and Horned puffins (Table 39).

The most common phonation in Tufted and Horned puffins was a short, low-pitched vocal "errr." I heard this sound only from birds within their nest-site, particularly when they were being disturbed, e.g., during my checking of their nests. Its primary function is probably as a threat or warning. However, in one instance, a Horned Puffin produced this sound when delivering the first load of fish to its newly hatched chick.

A second vocalization of Tufted and Horned puffins, was the "purring call." It was a low-pitched "errr" sound, similar to the threat call, but lasted several seconds longer. It was much softer in intensity than the threat call, having the low purring quality of a cat. Tufted Puffins repeated this call about every 20-35 sec for varying periods of time, whereas Horned Puffins allowed the call to trail off gradually and did not repeat it. The function of this vocalization is unknown, it was heard most frequently from birds resting on the colony.

A third vocalization of both Tufted and Horned puffins was the "bi-syllabic call," characterized by a short, sharp, and intense vocal

"er," followed immediately by a second syllable which was initiated in a higher pitched call note. For Tufted Puffins this second syllable trailed off gradually in pitch and intensity and was not repeated. Horned Puffins had an undulating pitch change associated with the second and final syllable. In Tufted Puffins this call was given more often on colony, but occasionally also by birds on water. In one instance, a member of a pair was sitting at the entrance to its burrow and gave this call about four times per minute consecutively for 1.5 hr. During this period, the bird's mate emerged from the burrow twice, and on one occasion billed with the calling bird.

The final "multi-note call" was the most complex. In Tufted Puffins, this call seemed to consist of a minimum of three syllables, with the third and final syllable being repeated many times. The third and following syllables were cyclic repetitions of the second syllable, and varied rhythmically in frequency and intensity giving the call a siren-like sound. This call was only heard from birds in their burrows, and no information was available as to the circumstances which initiated the call. In contrast, the multi-note call of Horned Puffins consisted of six and sometimes seven syllables. The first two syllables were identical with the bi-syllabic call previously described. However, the third syllable was higher in pitch than the others, and received the secondary stress of the entire utterance. The remaining three and sometimes four syllables more closely matched the initial vocal "er", (er errr er er er er er). This call was heard most frequently during the pre-egg stage and early incubation, and I suspect it may have had some sexual function.

Nest-site Preparation

Preparation of the nest-site prior to egg deposition in Tufted and Horned puffins involved three principal tasks: 1) excavation and cleaning of the nest site, 2) collection of nesting material, and 3) construction of the nest. Tufted Puffins spent considerable more time and effort in the excavation and cleaning of their nest-sites than Horned Puffins.

Earthen burrows, the typical nest-site used by Tufted Puffins, were damaged considerably from ice, snow, and rain during the winter periods of disuse. Hence, many Tufted Puffins had to re-excavate their burrows at the beginning of each breeding season. Birds sometimes began this task on the first day of their return to the colony; however, most excavation usually occurred a week or two later. Some burrows on both Buldir and Ugaiushak islands remained plugged with ice well into the pre-egg stage. Excavation of these burrows immediately followed the melting of the ice.

One or usually both members of a pair entered their burrow at least several times prior to excavation. Although both members of a pair may take part in the excavation, most of the work was consistently undertaken by the larger bird, presumably the male. Excavation was accomplished by the combined actions of the bill and feet. The bill was primarily used to excavate the sides and the top of the burrow by a combination of two processes. First, it was used as an axe or chisel to stab at the hard soil and knock it loose. Second, it was used as a pair of pliers to grasp chunks of soil and tear them

loose. The loose soil thus accumulated on the floor of the burrow was removed by a backward scraping motion of the feet. During this backward scraping, the long, sharp claws also deepened the burrow's floor. The power of the legs and feet during this scraping motion was impressive, with dirt being thrown at least 0.5 m into the air and out to a distance of greater than 1 m from the burrow entrance. The largest rock removed by an excavating bird measured 130 x 90 x 65 mm and weighed 1390 g, approximately twice the weight of the bird.

Burrow excavation usually lasted for only a few minutes at a time, though one bird might excavate several times in the same day. After each effort, the bird usually retreated to the sea to bathe.

Most pre-existing burrows were excavated to varying degrees by the breeding pair during the pre-egg stage and were sometimes reconstructed later in the breeding season. Such later excavation usually followed the loss of an egg, heavy rain, cave-ins, and/or frequent disturbance.

Tufted Puffins probably never use a burrow for breeding purposes in the same year that it is initially excavated. Initiation of new burrows by non-breeders may begin at any time during the breeding season but was most common in late July and August, several weeks after the first arrival of subadults. Apparently, subadult birds come to the breeding colony and dig their burrows at least one year prior to when they first breed. Whether these subadults are mated at this time or whether an individual digs the burrow independently is not known. Burrows may also be acquired by subadults or adults by taking over an abandoned burrow or by evicting the present owners,

although the latter alternative is rare.

Most burrows were cleaned during their yearly re-excavation. Tufted Puffin burrows that did not need re-excavation and most Horned Puffin rock crevice sites were also cleaned prior to the building of a new nest. Nest material, bits of egg-shell, fallen vegetation, and other debris which accumulated in the nest-site during the previous breeding season and winter were removed by the backward scraping action described above. Both sexes usually participated in nest cleaning, the whole operation taking only several bouts of a few minutes each.

First attempts to gather nesting material sometimes began several weeks prior to egg laying. Usually, however, Tufted and Horned puffins constructed their nests in the several days immediately prior to egg-laying.

The predominant nesting materials used by both species were grasses, stalks of umbels (Family Umbelliferae), and primary feathers of puffins and gulls, but some nests contained seaweed and bits of fishing line and netting. Nests of both species showed considerable variation in size which correlated roughly with the amount of vegetation in the immediate vicinity of the nest-site.

Nest-site Tenacity

Upon first land-coming each spring, pairs of Tufted and Horned puffins on Ugaiushak Island tended to associate with a particular nest-site which they subsequently used for breeding. Similarly,

Tufted and Horned puffins on St. Lawrence Island, AK, returned to their snow-covered nesting slopes and landed on top of the snow over their future nest-sites (Sealy 1973b). As nest-site tenacity had not been previously demonstrated for either of these species, I conducted an experiment to determine if Tufted Puffins use the same nest-site in successive years.

During the early incubation period of 1976, I captured and banded 15 incubating Tufted Puffins. Before returning each marked bird to its burrow I cut a small hole into the burrow's nest chamber through which subsequent observation could be made. The hole was plugged with sod between checks. Fifteen burrows in which chicks were raised in 1976 were used as controls. The adults of these control burrows were not handled nor were the burrows installed with an observation portal. Subsequent checks of the burrows containing marked birds in 1976 revealed that 14 of the 15 marked birds had deserted. Neither these birds nor their mates were seen again during that breeding season. Apparently, if one member of a pair deserts, the other does so as well.

During the incubation period of 1977, I checked each of the 15 experimental burrows for the presence of marked birds and each of the control burrows to determine if it was active or vacant. Only 7 of the original 15 experimental burrows contained an egg. I recaptured marked birds in 2 of these burrows. In both cases, the marked bird was recaptured in the same burrow in which it was originally marked. During checks of the other 5 experimental burrows either the same unmarked bird was caught repeatedly or the occupants flushed prior to

my arrival. By the end of the fifth day all of the birds associated with these burrows had deserted.

All 15 control burrows contained eggs in 1977, but it is unknown whether these were the same birds as in 1976.

These results from marked birds indicate that a minimum of 29% of those monitored exhibited nest-site tenacity. This is a minimum value since 5 additional burrows were active in 1977, but the presence of marked birds could not be determined. That all 15 control burrows were used in 1977 suggests that marking birds and/or installing observation portals in burrows was responsible for the desertion of 8 experimental burrows in 1977.

Although I collected no direct evidence to support nest-site tenacity in Horned Puffins, it is suggested by the number of Horned Puffin nests I found in exactly the same location in talus slopes and under beach boulders in successive years. Some of these nests were isolated by several hundred meters from their nearest neighbor. In light of the apparent availability of suitable nest-sites elsewhere, it seems unlikely that these nest-sites would be used by different pairs of birds in successive years.

Nest-site Competition and Cohabitation

Tufted and Horned puffins on Buldir and Ugaiushak islands shared their major nesting habitats with at least one other seabird species. The use of nesting space within each of these habitats was partitioned between species by the existence of microhabitats. While

the characteristics differentiating major habitats tended to be broad-based and obvious, e.g., earthen burrows in a seaslope versus rock crevices in a talus slope, characteristics differentiating microhabitats were more subtle, e.g., size differences of burrows or rock crevices within the same habitat.

To identify those species which may have been in potential competition with Tufted and Horned puffins for nest-sites, I first identified those species associated with each of the major habitats used by the puffins and second, I identified those species within each of these assemblages which either used or had the potential to use the same microhabitats as the puffins (Table 1).

I recorded species as breeding in a particular habitat if active nests containing either an egg or a chick of that species were observed in that habitat. Each habitat was searched at regular intervals throughout the breeding season. The determination of species associated with a particular microhabitat was more difficult. For example, rock crevices located deep within a talus slope were not accessible for observation. However, it was almost certain that these crevices varied widely in size. Based on the body size of the birds, it was possible to determine which species may potentially compete for the different sized crevices--the smaller the crevice size, the fewer species would be in potential competition (see Bedard 1969).

In situations where the microhabitats were observable, I considered species to be in potential competition if they occupied what appeared to be identical microhabitats. I considered two species in potential competition for nest-sites if they occupied the same burrow or rock crevice or if they occupied adjacent burrows of similar size.

Table 1. Species assemblages associated with nesting habitats used by Tufted and Horned puffins on Buldir and Ugaiushak islands.

TUFTED PUFFIN	
Nesting habitat, Buldir Island	Associated Species
Earthen burrows on seaslopes	Horned Puffin Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet Parakeet Auklet Rhinoceros Auklet[a] Ancient Murrelet
Rock crevices in bare and/or vegetated talus	Horned Puffin Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet Crested Auklet Least Auklet Parakeet Auklet Whiskered Auklet Ancient Murrelet
Earthen burrows at cliff-edge	Horned Puffin
Nesting habitat, Ugaiushak Island	Associated Species
Earthen burrows at cliff-edge	Rhinoceros Auklet Common Murre Thick-billed Murre
Rock crevices in bare and/or vegetated talus	Horned Puffin Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet[a] Parakeet Auklet Ancient Murrelet Common Murre Thick-billed Murre
HORNED PUFFIN	
Nesting habitat, Buldir Island	Associated Species
Rock crevices in bare and/or vegetated talus	Tufted Puffin Parakeet Auklet

Table 1. Continued

Nesting habitat, Buldir Island	Associated Species
Rock crevices in bare and/or vegetated talus	Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet Crested Auklet Least Auklet Whiskered Auklet Ancient Murrelet
Earthen burrows on seaslopes, inland hills, and banks of streambeds	Tufted Puffin Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet Parakeet Auklet Rhinoceros Auklet[a] Ancient Murrelet
Rock crevices under beach boulders	Whiskered Auklet Pigeon Guillemot
Rock crevices in cracks of cliff-face	none
Nesting habitat, Ugaiushak Island	**Associated Species**
Rock crevices in bare and/or vegetated talus	Tufted Puffin Fork-tailed Storm-Petrel Leach's Storm-Petrel Cassin's Auklet[a] Parakeet Auklet Ancient Murrelet Common Murre Thick-billed Murre
Rock crevices under beach boulders	Pigeon Guillemot
Rock crevices in cracks of cliff-face	none

[a]Species assumed to breed in habitat, although no eggs or chicks actually observed.

With the exception of rock crevices in cliff-faces, nest-sites did not appear to be limiting in any habitat, as many available nest-sites were not used. However, both Tufted and Horned puffins sometimes cohabited their nest-sites with another species. Such cohabitation in the presence of excess nest-sites poses the possibility that there may have been a further division of the microhabitat--that is, two species could use the same burrow without being in competition.

Fork-tailed Storm-Petrels commonly nested in small side tunnels within Tufted Puffin burrows. Similarly, Ancient Murrelets sometimes nested in side chambers in a puffin burrow without apparent rivalry between the two species. In one of these burrows, however, two Ancient Murrelet eggs were in the same nest with a Tufted Puffin egg. The three eggs were incubated for only one day (the identity of the incubating bird unknown), and then the nest was deserted. Also, I observed two instances of cohabitation of Parakeet Auklets with Tufted Puffins.

The cohabitation of Tufted Puffins with another species appears related to the daily activity patterns of other species. Of the three species observed cohabiting with the diurnal Tufted Puffin, the two nocturnal species, Fork-tailed Storm-Petrels and Ancient Murrelets, did so more frequently and with greater success than did the diurnal Parakeet Auklets. Similarly, on Destruction Island, WA, the nocturnal Rhinoceros Auklet sometimes nested successfully in the same burrow with Tufted Puffins (Frazer 1975).

Horned Puffins occassionally cohabited rock crevice nest-sites in talus slopes with Common Murres. Although not accessible for obser-

vation, I suspect that Horned Puffins regularly cohabit nest-sites with other crevice-nesting species in talus slopes.

THE EGG STAGE

Egg-laying Dates

To determine the egg-laying dates of Tufted and Horned puffins on Buldir and Ugaiushak islands, I examined marked nest-sites at regular intervals for the presence of an egg and back-dated known hatching dates by the length of the species' incubation period.

From marked nest-sites, I determined the egg-laying dates of 15, 51, and 142 Tufted Puffin eggs in 1975, 1976, and 1977, respectively. For Horned Puffins in 1975, I obtained the exact date one egg was laid, and I back-dated the known hatching dates of three other eggs by 42 days (Sealy 1969). In 1976, I obtained the laying dates of 22 Horned Puffin eggs by periodically searching a delineated area of talus for the presence of eggs. In 1977, laying dates of 44 Horned Puffin eggs were obtained by back-dating from known hatching dates.

Peak egg-laying of Tufted Puffins, the interval during which two-thirds of the sample birds laid, occurred 7-10 days earlier on Ugaiushak Island in 1976 and 1977 than on Buldir Island in 1975; however, the onset of laying occurred at about the same date in all years (Appendix I). Peak egg-laying of Horned Puffins occurred during the same period on Buldir Island in 1975 and Ugaiushak Island in 1977 but was several days later on Ugaiushak Island in 1976.

Although peak egg-laying of the two species overlapped in 1975, peak egg-laying of Horned Puffins followed that of Tufted Puffins by 1-2 weeks in 1976 and 1977.

In all years, egg-laying of Horned Puffins appeared to be more synchronous than that of Tufted Puffins. While the length of egg-laying including replacement clutches generally lasted about 1 mo. for each species, two-thirds of the sample population of Tufted and Horned puffins layed within a 2-and 1-week period, respectively.

Although there is little information on the timing of egg-laying of Tufted Puffins at their northern breeding limits, peak egg-laying is apparently about 1 mo earlier at their southern breeding limits (Appendix I). Peak egg-laying of Horned Puffins, on the other hand, occurs about only 2 weeks earlier in their southern breeding areas (Appendix I). At the same latitude, peak egg-laying is generally 1-3 weeks earlier for Tufted than Horned puffins. In general, peak egg-laying over the geographic range of Tufted Puffins occurs between the last week of May and mid-June while that of Horned Puffins is typically between mid-June and the first week of July.

Accessibility of nest-sites appeared to influence the timing of egg-laying in Tufted Puffins in each of the 3 years of my study. When the Tufted Puffins first arrived in May, many burrows contained ice, standing water, or mud. Egg-laying generally began 3-4 weeks after the arrival of the birds. By this time most burrows had "dried-out" and their substrate temperature had risen from approximately 2° C to 9° C (Table 2). These dry burrows were the first to have eggs laid in them. Wet burrows had eggs laid in them immediately after

Table 2. Temperature (C°) of burrow substrate just prior to arrival, during egg-laying, and during hatching for Tufted Puffins on Ugaiushak Island, 1977.

	Pre-Arrival 4 May	Egg-laying 4-12 June	Hatching 16-23 July
N	65	23	4
$\bar{x}$	2.1	9.0	14.5
Max.	4.0	10.5	15.5
Min.	0 (ice)	7.5	13.0

they dried out, suggesting that egg-laying was delayed in these burrows.

Delayed laying in Horned Puffins was not observed in any year, probably because rock crevices had better water drainage than did earthen burrows, thus avoiding the necessity of delayed laying in this species.

For 1976 and 1977, I compared the rank order of egg-laying in 12 Tufted Puffin burrows between years. In 9 of these 12 burrows, the order of egg-laying was the same each year. Assuming nest-site tenacity, this shows a strong tendency for pairs to lay at the same date relative to the rest of the population from year to year. Alternatively, and not assuming nest-site tenacity, the burrows became available in the same order each year.

Egg Description

Previous descriptions of Tufted and Horned puffin eggs have been made from relatively small sample sizes (Grinnell 1900, Bent 1919, Dement'ev and Gladkov 1951, Kozlova 1957, Sealy 1973, Amaral 1977, Moe and Day 1979). In particular few fresh egg weights have been reported and no studies have been conducted to determine the degree of egg weight loss during natural incubation, although Manual and Boersma (1978) measured egg weight loss in Tufted Puffins using a bantam hen for incubation. During the course of this study I had the opportunity to measure and observe variations in the shape, color, and markings of 124 Tufted Puffin and 72 Horned Puffin eggs. Also, in

1977, I measured egg weights during incubation for 9 Tufted Puffin and 5 Horned Puffin eggs.

Maximum length and maximum width were measured with vernier calipers to the nearest 0.1 mm. Only the weight of eggs less than 3 days old was taken; they were measured to the nearest 0.5 g with a 100 g or 200 g Pesola spring balance. Tests for significant differences in the size of Tufted and Horned puffins eggs were made using a Student's t-test at $p < 0.05$. Egg weight, expressed as percent of adult body weight (proportionate egg weight), for each sex was determined by taking the mean fresh egg weight and dividing this value by the mean adult body weight of each sex, averaged for all members of that sex collected throughout the breeding season that year. The percent of egg weight loss during the incubation period was computed by subtracting the weight of starred or pipped eggs from their original weights and dividing this difference by their original weights.

Tufted and Horned puffin eggs were ovate in shape with a tendency toward ovate-pyriform. Eggs of both species showed considerable individual variation in color and markings. In general, eggs were a dull creamy-white or pale bluish-white with many showing a variable number of spots and/or scrawls of gray, blue, green, reddish-brown, and brown. In most cases, these spots and/or scrawls tended to form a wreath aroung the large end of the egg. A slightly higher percentage of Horned than Tufted puffin eggs had a background more deeply colored greenish-blue and bolder markings of spots and especially scrawls.

The length, width, and weight of eggs within each species were not significantly different between the two islands, nor between years on Ugaiushak Island (Table 3). Tufted Puffin eggs were significantly longer, wider, and heavier than Horned Puffin eggs in all 3 years (Table 3); however, proportionate egg weight was significantly lower for Tufted than Horned puffins (Table 4). Similar values of proportionate egg weight for Tufted Puffins, 11.4% and 11.8%, have been reported by Sealy (1973a) and Amaral (1977), respectively. However, both of these authors report lower values of proportionate egg weight than I observed for Horned Puffins, 9.5% and 12.3%, respectively. These discrepancies are probably attributable to the significantly larger size of adult Horned Puffins on St. Lawrence Island, AK, (Sealy 1973a) and to the small sample size used by Amaral (1977).

The mean egg weight loss of 12-13% during incubation was not significantly different between Tufted and Horned puffins (Table 5). Using a bantam hen to incubate five Tufted Puffin eggs, Manuwal and Boersma (1978) found a mean egg weight loss in this species of 17%.

Egg Twinning

Although Tufted and Horned puffins generally lay a single egg clutch, both species develop two separate and distinct laterally placed brood patches, suggesting some time in their evolutionary past they laid two eggs (Fisher and Lockley 1954; Wynne-Edwards 1955, 1962; Lack 1954). Presumably, selection in these species has acted to favor the laying of one egg in modern times. But if given two eggs, will birds choose to only incubate one?

Table 3. Measurements of Tufted and Horned puffin eggs from Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

	Buldir Island 1975			Ugaiushak Island 1976			Ugaiushak Island 1977		
	Weight (g)	Length (mm)	Width (mm)	Weight (g)	Length (mm)	Width (mm)	Weight (g)	Length (mm)	Width (mm)
Tufted Puffin									
$\bar{x}$	94.4	72.5	49.3	94.7	72.9	49.3	93.9	73.5	49.0
s	7.48	3.05	1.48	7.79	3.18	1.47	5.67	2.53	1.57
Max.	107.5	80.5	52.0	110.0	79.0	52.0	107.0	79.8	51.9
Min.	81.0	68.5	46.4	81.0	68.5	46.5	81.5	68.6	46.3
N	37	37	37	41	41	41	39	46	46
Horned Puffin									
$\bar{x}$	76.2	56.2	45.8	75.6	67.2	45.9	74.8	66.7	45.6
s	4.75	2.59	1.29	4.11	2.30	1.07	5.61	2.91	1.40
Max.	86.5	71.6	47.6	81.5	71.6	47.6	84.0	72.2	47.5
Min.	68.5	62.7	42.8	68.5	62.7	43.9	63.0	60.6	42.6
N	18	19	19	17	17	17	36	36	36

Table 4. Egg weight as percent adult body weight for Tufted and Horned puffins on Buldir Island, 1975 and Ugaiushak Island, 1976 and 1977.

Location	Egg Weight (g) N	Mean	Range	Body Weight (g) Sex	N	Mean	Range	Percent of adult body weight
Tufted Puffin								
Buldir Island 1975	37	94.4	81.0-107.5	M	42	775	732-850	12.1
				F	37	733	643-862	12.9
Ugaiushak Island 1976	41	94.7	81.0-110.0	M	14	814	740-896	11.6
				F	14	740	678-862	12.8
Ugaiushak Island 1977	39	93.9	81.5-107.0	M	6	863	769-986	10.9
				F	-	-	-	-
Horned Puffin								
Buldir Island 1975	18	76.2	68.5-86.5	M	23	508	415-602	15.0
				F	42	483	415-550	15.8
Ugaiushak Island 1976	17	75.6	68.5-81.5	M	5	564	506-594	13.4
				F	10	510	445-559	14.8
Ugaiushak Island 1977	36	74.8	63.0-84.0	M	1	540	-	13.9
				F	5	518	493-536	14.4

Table 5. Egg weight loss for Tufted and Horned puffins on Ugaiushak Island, 1977.

	Starting egg weight (g)	Final egg weight (g)	Egg weight loss (g)	Egg weight loss (%)	Length of time (days)
Tufted Puffin (N=9)					
$\bar{x}$	95.0	82.5	12.6	13.2	45.3
s	6.04	4.89	2.03	1.62	4.09
Max.	102.0	90.0	16.5	16.2	52
Min.	86.0	75.0	10.0	10.9	42
Horned Puffin (N=5)					
$\bar{x}$	76.8	67.5	9.3	12.1	36.4
s	4.55	4.51	1.68	2.12	2.19
Max.	84.0	75.0	10.5	13.8	38
Min.	73.0	63.0	6.5	8.9	34

To answer this question, I placed an additional puffin egg (making a clutch of two) in each of ten Tufted Puffin nests at the onset of incubation. I then checked each of these nests at least once weekly throughout the incubation period to see which eggs in each nest were (warm) and were not (cold) being incubated.

In three nests, each egg was incubated alternately, but not simultaneously. None of these eggs hatched. In five nests, one egg was incubated consistently, and the other egg was either pushed aside in the nest chamber or was at some point removed from the burrow. Three of these nests hatched chicks and the other two were deserted after 47 days. All five of the eggs that were incubated were the added, not the original, eggs. In the remaining two nests, both eggs were deserted shortly after the experiment began.

The fact that both eggs were not incubated simultaneously in any of the ten nests suggests that, concomitant with the selective forces favoring the laying of one egg rather than two, Tufted Puffins also choose to incubate one egg rather than two.

Egg Replacement

Tufted and Horned puffins typically lay a single, one-egg clutch each breeding season. Replacement laying after the loss or abandonment of the first clutch has been suggested for Tufted Puffins by Dement'ev and Gladkov (1951), Kozlova (1957), and Amaral (1976) and for Horned Puffins by Swartz (1966). To test this possibility, I removed freshly-laid eggs from ten Tufted Puffin and ten Horned

Puffin nests on Ugaiushak Island in 1977. After removing these eggs, I regularly checked each of the nests for signs of re-nesting activity (i.e., re-excavation, nest-building) and for the appearance of a replacement egg.

The incidence of replacement laying and the interval between egg removal and the appearance of replacement eggs are shown in Table 6. Seven of the Tufted Puffin burrows were re-excavated within a week following removal of the first egg, and five of these subsequently contained a replacement egg. For Tufted Puffins, I also removed the first replacement eggs and continued to monitor those nests for the appearance of a second replacement clutch. None of the seven burrows containing first replacement eggs were re-excavated following the removal of the replacement clutches. All eggs involved in the experiment were weighed and measured to determine if replacement eggs differed from those in the first clutches.

Two Horned Puffins nests were rebuilt following removal of the first eggs, and one of these subsequently contained a replacement egg. All three of the Horned Puffin nests containing replacement eggs were abandoned shortly after the second egg was laid. One of these nests, however, contained an additional egg 6-18 days following the first replacement egg, suggesting the possibility of a third clutch by the same pair of birds.

In Horned but not Tufted puffins, the weight and volume of the first eggs were significantly ($p < 0.05$, Wilcoxon Signed Ranks Test) greater than those of replacement eggs (Table 7).

Table 6. Replacement laying in nests from which eggs were removed for Tufted and Horned puffins on Ugaiushak Island, 1977.

	TUFTED PUFFIN	HORNED PUFFIN
Number nests from which eggs were removed	10	10
Number nests with eggs relaid once	7	3
Number nests with eggs relaid twice	0	1 (?)
Days between egg removal and relay	10-21	16-20

Table 7. Measurements of first egg and replacement egg of Tufted and Horned puffins on Ugaiushak Island, 1977

	Nest-egg #	Weight (g)	Length (mm)	Width (mm)	Index of egg volume[a] (cm^3)
Tufted Puffin					
	a-1	91.5	75.8	47.8	173.2
	a-2	86.5	71.1	47.6	161.1
	b-1	89.5	68.6	48.8	163.4
	b-2	79.0	68.9	46.6	149.6
	c-1	95.5	76.9	48.0	177.2
	c-2	93.0	77.4	47.4	173.9
	d-1	100.5	74.5	50.4	189.2
	d-2	95.5	75.5	48.0	174.0
	e-1	97.0	75.1	48.8	178.9
	e-2	98.0	74.9	49.5	183.5
	f-1	96.5	72.0	50.0	180.0
	f-2	97.0	73.8	49.9	183.8
	g-1	88.5	72.3	47.5	163.1
	g-2	89.0	72.9	47.5	164.5
Horned Puffin					
	a-1	84.0	67.8	47.3	151.7
	a-2	75.0	65.0	45.9	136.9
	b-1	74.0	67.3	46.2	143.7
	b-2	69.0	65.1	44.5	128.9
	c-1	78.5	65.0	47.5	146.7
	c-2	74.5	65.0	45.4	134.0

[a]Index of Egg Volume = length x (greatest width)^2

The validity of these experiments rests on the assumption that the same pair of birds was responsible for each of the eggs laid at an experimental nest-site. The fact that nest-sites did not appear limiting to either species (see above) lends credibility to this assumption.

The observed frequency of replacement laying for both Tufted and Horned puffins represents a minimum potential, in that nests which did not have a replacement egg may have been deserted as the result of human disturbance during the experiment.

Brood Patches

Previous data on the size of completely developed brood patches in Tufted and Horned puffins have been based on one Tufted Puffin (Amaral 1977), and four Horned Puffins (Sealy 1973a), and nothing has been known about the timing of brood patch development and subsequent refeathering.

On Buldir Island in 1975, I examined the progression of brood patch development and subsequent regression throughout the breeding season of Tufted and Horned puffins. Between 17 May and 21 August and 28 May and 21 August, I collected 78 Tufted Puffins and 65 Horned Puffins, respectively, for stomach content analysis. The brood patch for each specimen was scored according to the following system of classification (based on Sealy 1972):

Class 0 - No evidence of defeathering.

Class 1 - Loss of most contour feathers and some down.

Class 2 - Complete loss of contour feathers and down, heavy vascularization. (Maximum development).

Class 3 - Regression beginning; down appearing around edges; sheaths of new coutour feathers appearing.

Class 4 - Regression nearly complete; area covered with down and contour feathers breaking out of sheaths.

Class 5 - Complete regression; same appearance as Class 0.

The length and width of Class 2 brood patches were measured with vernier calipers to the nearest 1 mm.

Left and right brood patches showed no significant ($p > 0.05$, t-test) difference in size for either Tufted or Horned puffins. Brood patches of Tufted Puffins were slightly larger in size than those of Horned Puffins (Table 8), correlating with their larger eggs.

Defeathering apparently began several days before egg-laying (Table 9). None of the 15 Tufted Puffin specimens examined between 28 May and 4 June showed any defeathering, but between 5 and 14 June, 10 (83%) of the 12 Tufted Puffins collected possessed Class 2 brood patches (maximum development). Six (55%) of the 11 Horned Puffins collected during this time had Class 2 brood patches and 1 (11%) had a Class 1 patch.

By the end of the incubation period, over 50% of the Tufted and Horned Puffins collected showed evidence of refeathering. Refeathering continued throughout the nestling period, but only a few birds had attained complete regression when the last collection was made on 21 August.

Table 8. Measurements of Tufted and Horned puffin Class 2 brood patches.

		Length (mm)		Width (mm)	
	N[a]	$\bar{x}$	s	$\bar{x}$	s
Tufted Puffin	26	62.4	8.06	24.5	3.13
Horned Puffin	19	57.4	8.45	23.1	2.87

[a]N = The number of birds for which one brood patch was measured.

Table 9. Frequency of brood patch classes observed at different phenological periods during the breeding season for Tufted and Horned puffins on Buldir Island, 1975.

	Brood Patch Class						
	0	1	2	3	4	0/5	Mean
Tufted Puffin							
Pre-egg Stage							
17 May-4 June	15(100%)						0
Egg-laying and Incubation Stages							
5 June-14 June		2(17%)	10(83%)				1.8
15 June-30 June			10(100%)				2.0
1 July-15 July			5(46%)	5(46%)		1(8%)[a]	
Hatching and Nestling Stages							
16 July-31 July				1(25%)	3(75%)		3.8
1 August-14 August					1(100%)		4.0
15 August-21 August				1(4%)	22(88%)	2(8%)[a]	4.1

Table 9. Continued

	Brood Patch Class						
	0	1	2	3	4	0/5	Mean
Horned Puffin							
Pre-egg Stage							
28 May-4 June	8(89%)	1(11%)					0.1
Egg-laying and Incubation Stages							
5 June-14 June	4(36%)	1(9%)	6(55%)				1.2
15 June-30 June		10(100%)					1.0
1 July-20 July			4(36%)	4(36%)	3(28%)		2.9
Hatching and Nestling Stages							
21 July-31 July				2(22%)	7(78%)		3.8
1 August-14 August					4(100%)		4.0
15 August-21 August				1(10%)	6(60%)	3(30%)[a]	4.2

[a]It is unknown whether these birds developed brood patches during the breeding season.

Incubation Rhythm

Both male and female Tufted and Horned puffins participate in incubation (Dement'ev and Gladkov 1951, Kozlova 1957, Amaral 1977). There has been little information collected on the incubation rhythm of the adults (Kozlova 1937, Wehle 1976, Amaral 1977), i.e., the length of time one parent sits on the egg before being relieved by its mate. Data from these studies, as well as information from Ugaiushak Island in 1976 and 1977, indicate that, at least for Tufted Puffins, there is both intercolony and intra-colony variation in incubation rhythms.

For Tufted Puffins on the Barren Islands, AK, Amaral (1977) found that most frequently the incubating adult was relieved by its mate between 04:00-09:00 Alaska Standard Time, again in mid-afternoon, and usually again prior to nightfall. However, it was not unusual for the same bird to incubate throughout an entire day or for it to leave its egg unattended for several hours a day while it loafed with its mate outside the burrow. Occasionally, eggs were left unattended for a day or more. I observed this same general pattern on Ugaiushak Island in 1976 and 1977. However, the pattern was different on Buldir Island in 1975, where semi-cyclic colony attendance throughout the incubation period indicated an incubation rhythm of 4-5 days (Wehle 1976).

For Horned Puffins, Amaral (1977) reported adults exchanging incubation duties in the early evening, when maximum numbers of birds were present on the colony. However, non-incubating birds frequently visited their nesting crevices during the day, so it is

possible that incubation duties were exchanged more frequently than once a day. I observed a similar incubation rhythm in Horned Puffins at both Buldir and Ugaiushak islands. Like Tufted Puffins, Horned Puffins left their egg unattended for several hours a day, incubated for up to a day or more apparently without relief, and occassionally left the egg unattended for at least one day.

The incubation rhythm of seabirds depends, in part, on the distance the adults must travel from the colony to obtain food and the difficulty they have in obtaining that food (Ashmole and Ashmole 1967, Lack 1968, Ashmole 1971, Sealy 1976). The intercolony variations in incubation rhythms in Tufted Puffins is probably the result of variations in food availability (see "Feeding, Food, and Growth of Nestlings"). The lack of intercolony variation in Horned Puffins is probably related to their feeding inshore.

Length of Incubation

Prior to the initiation of this study, the length of incubation in Tufted Puffins was unknown, although Sealy (1972) estimated it to be about 45 days. In 1976 and 1977, I determined the length of incubation for 35 Tufted Puffin eggs for which both the date of laying and the date of hatching were known to the nearest day. The mean incubation period for these eggs was 46.5 days (range: 42 to 53 days). In a study also conducted in 1976, Amaral (1977) reported a mean incubation period for 11 Tufted Puffin eggs of 45.2 days (range: 43 to 53 days).

The length of the incubation period in Horned Puffins is slightly shorter than in Tufted Puffins. For five eggs, Sealy (1969) found a mean incubation period of 41.4 days (range: 40-43 days) and Amaral (1977) for five eggs reported a mean incubation period of 40.2 days (range: 39 to 42 days).

Variation in the length of the incubation may be the result of several factors. Although Tufted and Horned puffins in my studies generally began continuous incubation on the day the egg was laid, both species, and especially Tufted Puffins, occasionally did not begin continuous incubation until up to 4 days after the egg was laid. Also, individuals of both species left their eggs unattended for a day or more during incubation (see "Incubation Rhythms"). Finally, there was considerable individual variation in the length of the hatching period, the interval between first starring of the egg and total emergence of the chick (Table 10). There was no significant difference (p 0.05, t-test) in the length of the hatching period between species.

THE NESTLING STAGE

Aspects of the nestling stage of Tufted and Horned puffins are discussed in this section; however, information on the growth and development of chicks is discussed in the section entitled "Feeding, Food, and Growth of Nestlings."

Table 10. Length of hatching period[a] (days) for Tufted and Horned puffin eggs on Ugaiushak Island in 1976 and 1977.

Stage of Hatching	Year	N[e]	Mean	Range
Starred[b] to Pipped[c]				
Tufted Puffin	1976	3	3.0	2 to 4
	1977	11	3.1	1 to 8
Horned Puffin	1977	1	4.0	
Pipped to Total Emergence[d]				
Tufted Puffin	1976	5	1.4	1 to 2
	1977	19	2.3	1 to 5
Horned Puffin	1977	2	3.5	3 to 4
Starred to Total Emergence				
Tufted Puffin	1976	7	3.3	2 to 6
	1977	16	4.3	1 to 12
Horned Puffin	1977	2	3.0	2 to 4

[a]Hatching period: defined as interval between the first day egg is starred and the day of total emergence of chick from shell.

[b]Starred: defined as egg shell having fractures but not complete hole through shell.

[c]Pipped: defined as eggshell having a complete hole through shell.

[d]Total Emergence: defined as chick completely out of egg shell.

[e]The numbers do not necessarily represent the same individual eggs in different stages of hatching.

Hatching

Hatching of Tufted and Horned puffin chicks is aided by a single egg tooth located on the tip of the upper mandible. The egg tooth generally disappears gradually within several weeks after hatching although it sometimes drops off abruptly (Table 11).

Adult Tufted and Horned puffins typically remove the eggshell from the nest within 3 days after the chick hatches, thus keeping the relatively small nest-site clean and free of debris.

Brooding Period

Most Tufted Puffins brooded their chick more or less continuously for 1-3 days after hatching, although I found unattended chicks less than 1 day old a number of times. I never found adults present in burrows with chicks over 3 days old, except when they were delivering food. Similarly, Cody (1973) and Amaral (1977) reported Tufted Puffins attending their chicks for 3-5 days and 0-4 days after hatching, respectively.

Horned Puffins typically brooded their chick continuously for 5-7 days after hatching. Thereafter, I observed adults in nest-sites only when delivering food. In five Horned Puffin nests studied, Amaral (1977) found that adults attended their chicks for an average of 6.7 days after hatching.

Presumably, the termination of brooding reflected the ability of the nestlings to thermoregulate on their own. Sealy (1968) found that

Table 11. Age (weeks) at which the egg tooth disappeared in Tufted and Horned puffin chicks on Ugaiushak Island, 1976 and 1977 combined.

Chick age	Number of chicks	
	Tufted Puffin (N=27)	Horned Puffin (N=28)
1	1 (3.7%)	1 (3.6%)
1-2	6 (22.2%)	16 (57.1%)
2-3	13 (48.1%)	9 (32.1%)
3-4	4 (14.8%)	2 (7.1%)
4	3 (11.1%)	0

a Horned Puffin nestling was able to maintain its initial body temperature after being exposed to ambient temperatures of 9° C for 50 min at the age of 6 days, the age at which Amaral (1977) and I found that adults terminated brooding.

Color Phases of Tufted Puffin Nestlings

The typical coloration of Tufted Puffin belly feathers in the downy and juvenal plumages is black and various shades of gray, respectively. The existence of white-bellied birds has been reported by Stejneger (1885), Dawson (1940), and Dement'ev and Gladkov (1951). The frequency with which white-bellied birds occur in the population, however, has not been previously reported.

Of 81 downy chicks examined on Ugaiushak Island in 1976 and 1977, 5 (6.2%) had white belly down (Table 12). A similar frequency was observed on the Barren Islands, AK, (Table 12). White belly down varied from a patch approximately 20 mm in diameter to patches covering virtually the entire belly.

Of 34 chicks in juvenal plumage, 8 (23.5%) had white bellies. Again, almost an identical frequency of white bellies in juvenal plumage was observed on the Barren Islands (Table 12).

Length of the Nestling Period

Only a small percentage of the Tufted and Horned puffin nestlings had fledged by the time I left the study area in late August-

Table 12. Frequency of color phases in the downy and juvenal plumages of Tufted Puffins on Ugaiushak Island 1976 and 1977, and the Barren Islands, 1977 (M. J. Amaral, pers. comm.)

		Ugaiushak Island						Barren Islands	
		1976		1977		Total		1977	
		No.	%	No.	%	No.	%	No.	%
Downy plumage (belly down)	White	2	5.7	3	6.8	5	6.2	1	2.5
	Gray	35	94.3	41	93.2	76	93.8	39	97.5
Juvenal plumage (belly contour feathers)	White			8	23.5			8	25.0
	Gray			26	76.5			24	75.0

early September each year (Table 13). Accurate data on the length of the nestling period--the interval from the total emergence of the chick at hatching to the permanent departure of the chick from the nest-site--was obtained for nine Tufted Puffin chicks in 1976 and four in 1977. Both the date of hatching and the date of fledging of these chicks were known to the nearest day. The mean length of the nestling period for these chicks was 44.8 ± 2.1 days in 1976 and 41.8 ± 1.9 days in 1977.

Tufted and Horned puffins both exhibit considerable intraspecific variation in the length of the nestling period (Table 46). Variations in nestling period length are correlated with the rate of growth of the chicks, which in turn are determined by a concert of factors related to the food and feeding of young (see "Food, Feeding, and Growth of Nestlings").

Departure of Fledglings

Tufted and Horned puffin chicks fledge at night or in the early morning. Fledging at night has probably developed in response to predation from diurnal avian predators (Sealy 1972, Amaral 1977).

On Buldir and Ugaiushak islands, there were a few locations where chicks could walk to the sea from their nest-sites, however, most chicks probably jumped or fluttered to the sea from the cliff-tops or seaslopes. Apparently, most fledglings are flightless at the time of their departure (Amaral 1977).

Table 13. Fledging age (days) for Tufted and Horned puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

		TUFTED PUFFIN			HORNED PUFFIN	
		Buldir Island 1975	Ugaiushak Island 1976	Ugaiushak Island 1977	Buldir Island 1975	Ugaiushak Island 1977
Total number of nestlings monitored		2	27	10	2	10
Number of nestlings fledged[a]		0	9 (33%)	4(40%)	0	0
Age of nestlings fledged[a]	mean		44.8	41.8		
	oldest		48	42		
	youngest		40	41		
Number of nestlings not fledged[a]		2 (100%)	18 (67%)	6 (60%)	2 (100%)	10 (100%)
Age of nestlings not fledged[a]	mean	42.0	44.0	36.7	42.0	27.8
	oldest	46	48	41	43	34
	youngest	36	40	32	41	17

[a]by last check: 1975=3 September, 1976=2 September, 1977=27-28 August

Once on the water, fledglings swam immediately out to sea. Adults whose chicks had fledged continued to return to the breeding colony for several days afterwards, suggesting that once chicks fledge they are entirely self-sufficient.

BREEDING SUCCESS

In the following discussion, breeding success is considered in terms of three components of success: 1) laying success, the percent of the total number of nest-sites monitored, active and inactive, which contained eggs; 2) hatching success, the percent of the total number of eggs laid which hatched; and 3) fledging success, the percent of hatched chicks which survived to fledging.

I determined the laying success of Tufted Puffins each year by regularly checking all burrows within a specified area for the presence of eggs. Once an egg was located, it was not checked again until it was due to hatch. Laying success of Horned Puffins could not be determined due to the difficulty of identifying individual nest-sites prior to egg deposition.

Each year I observed a number of burrows which had Tufted Puffins associated with them, but which never contained eggs. To determine the proportion of burrows which were unoccupied or were occupied by breeding or by non-breeding puffins, I monitored the activity of 35 randomly selected burrows from a nearby blind for several hours a day, 2-7 days a week, throughout the 1977 breeding season. These burrows were checked periodically for presence of eggs

and chicks and birds associated with each burrow were recognized by unique morphological or behavioral characteristics.

Hatching success of Tufted Puffins was determined by checking known age eggs regularly after about 40 days of incubation. For Horned Puffins, in 1977 I periodically checked 1976 nest locations early in the season for eggs. Once an egg was located, usually within a week of laying, it was checked regularly beginning about 30 days after it was first located.

Few or no monitored Tufted Puffin chicks fledged by the time I left the island each year. Therefore, I have estimated fledging success based on the proportion of initial nestlings monitored which fledged or were of fledging weight at the time of my departure. Fledging success was based on chicks from a number of study burrows and not just those hatched from eggs used to determine hatching success.

I considered a bird to be of fledging weight if its weight was equal to or exceeded the minimum weight of any chick known to have fledged in 1976 and 1977. This value was 496 g, or approximatley 64% of adult body weight. I have incorporated the possibility of survival or mortality of those chicks not at fledging weight at the time of my departure by expressing fledging success and chick mortality as ranges. The minimum value of chick mortality represents that proportion of chicks known to have died or disappeared prior to my leaving the island.

None of the Horned Puffin chicks monitored in 1975 or 1977 fledged before I left the island. Estimates of fledging success were

determined in the same manner as for Tufted Puffins. Fledging weight was taken as 400 g or approximately 67% of adult body weight, the lowest fledging weight reported by Amaral (1977).

Laying success of Tufted Puffins was relatively consistent between years, ranging from 48-59% (Table 47). Similar values of laying success, 47% and 56%, were observed on the Barren Islands, AK, by Amaral (1977) and Manuwal and Boersma (1978), respectively. The highest value of laying success, 76%, has been reported on Sitkalikdak Island, AK, (Baird and Moe 1978). I suspect the average laying success of Tufted Puffins is 50-60%, considering intercolony and annual variations.

Of 35 study burrows on Ugaiushak Island in 1977, 16 (46%) had eggs laid in them, 4 (11%) never had any birds associated with them, and 15 (43%) had birds associated with them during all or part of the breeding season but never contained eggs (Table 14). Further, throughout the breeding season, only approximately 50% of the birds present on the colony were actively engaged in breeding at any point in time (Table 14).

Hatching success of Tufted Puffins in monitored burrows increased significantly each year from 19% in 1975 to 83% in 1977, probably in large part because progressively better monitoring techniques resulted in fewer desertions. Paramount among these improvements were: 1) the marking of all burrows and the installation of all observation holes before egg-laying, 2) the use of smaller observation holes plugged with sod rather than plywood, and 3) a reduction of investigator time on the colony during the incubation stage.

Table 14. Summary of breeding success and burrow use of Tufted Puffins throughout the breeding season on Ugaiushak Island, 1977.

35	total burrows in study plot		
4 (11%)	never had birds associated with them		
31 (89%)	had birds associated with them at some point during the breeding season		
	12 (39%)	hatched chicks	
	4 (13%)	had eggs laid in them but did not hatch chicks	
		2 (50%)	were deserted immediately after the egg was laid and the adults were not associated with the burrow throughout the remainder of the breeding season
		2 (50%)	were deserted later in incubation and at least one of the adults was associated with the burrow throughout the remainer of the breeding season
	15 (48%)	never had eggs laid in them	
		7 (47%)	had birds associated with them only during the pre-egg/egg-laying stage
		8 (53%)	had birds associated with them throughout the breeding season

Hatching success of Tufted Puffins at other colonies has ranged from 4.3-100% (Wehle, Chapter II, Table 47), with an average success rate for the 13 colony-years of roughly 55-60%. As the influence of human disturbance on hatching success could not be determined, I suggest a natural hatching success rate of 75-90%.

Aside from human disturbance, egg mortality of Tufted Puffins has several other causes. Some puffin eggs on Buldir and Ugaiushak islands were eaten by Glaucous-winged Gulls (Larus glaucescens) and Common Ravens (Corvus corax) but egg mortality was minimal in all 3 years due to the inaccessibility of puffin nest-sites to the predators. In 1975, only 3 (1.3%) of 225 Glaucous-winged Gull pellets examined contained eggshell fragments. Even these shells may have been from deserted or discarded eggs. Ravens probably took more eggs than gulls as they sometimes excavated through the thin layer of topsoil over the nest chamber to reach the egg.

Glaucous-winged Gulls and Peregrine Falcons (Falco peregrinus) on both islands also contributed indirectly to puffin egg mortality. Alarm calls from these birds frequently caused panic flights by puffins, causing a number of broken or displaced puffin eggs.

Predators of Tufted Puffin eggs reported in other colonies include crows (Corvus sp.) (Vermeer 1978), River Otters (Lutra canadensis) (Lehnhausen 1980), and Arctic Foxes (Alopex lagopus) (R. H. Day, pers. comm.).

As Tufted Puffins typically nest in earthen burrows, their eggs are vulnerable to flooding. During each year of my study, a small proportion of eggs laid were eventually deserted as a result of being buried in mud.

In 1977, over half of the observed egg mortality was due to infertile eggs or to the death of embryos during hatching. Similarly, M. J. Amaral (pers. comm.) observed significant egg mortality in Tufted Puffins during hatching.

Finally, a proportion of Tufted Puffins desert their eggs each year for unknown reasons. Manuwal and Boersma (1978) suggested a 5-10% natural desertion rate in Tufted Puffins, while my observations indicate a slightly higher rate of perhaps 5-15%.

Hatching success of Horned Puffins was 76% on Ugaiushak Island in 1977. Hatching success in other colony-years ranged from 56-100% with an average of roughly 80% (Wehle, Chapter II, Table 48). The higher hatching success of Horned than Tufted puffins is probably more apparent than real, reflecting more the methodological differences employed in monitoring nest-sites in different habitats. From my own experience, Horned Puffins deserted less frequently than Tufted Puffins, because individual nest-sites were subjected to less disturbance during monitoring. To check Tufted Puffin burrows it was necessary to install observation portals which had to be opened during each check, whereas almost all Horned Puffin nests could be viewed from a distance, thus not causing attending adults even to move from the nest. Hence, the values for Horned Puffin hatching success are probably more nearly representative of natural (undisturbed) populations.

Horned Puffins on Buldir and Ugaiushak islands were subject to the same disturbance and predation by other birds as Tufted Puffins. In all years, however, the contribution of these influences on egg mortality was minimal. On the Shumagin Islands, AK, Arctic Foxes

have been observed to prey heavily on Horned Puffin eggs (R. H. Day, pers. comm.).

Owing to the better drainage of rock crevice habitats, especially talus slopes, flooding was not an important factor in Horned Puffin egg mortality. As with Tufted Puffins, most Horned Puffin egg mortality on Ugaiushak Island in 1977 was due to infertility or to death of the embryo while hatching. On the Barren Islands, AK, one of three Horned Puffin eggs which failed to hatch was infertile (Amaral 1977).

Minimum estimated fledging success of Tufted Puffins was 0% in 1975 on Buldir Island and 80% in 1976, and 62% in 1977 on Ugaiushak Island (Table 15). The minimum value of estimated fledging success probably reflects the true success rate in 1975, while the maximum values of estimated fledging success (Table 15) reflect the actual success rates in 1976 and 1977. In these latter two years, all observed nestling mortality occurred when chicks were less than two weeks old. That most chick mortality occurrs in chicks less than two weeks old has also been observed in other puffin species (Myrberget 1962, Nettleship 1972, Ashcroft 1976, Wilson 1977).

In the absence of terrestrial predators, the most likely potential cause of death in older chicks is lack of food. As there was no evidence to suggest insufficient food availability to chicks in either 1976 or 1977 (see "Food, Feeding, and Growth of Nestlings"), I suspect that all chicks not fledged by the time of my departure in these two years did so successfully at a later date. On the other hand, the two chicks monitored on Buldir Island in 1975 grew much more slowly than chicks reported in any other colony (see "Growth Rates of Nestlings"). Therefore, I consider it unlikely that either of these chicks fledged.

Table 15. Fledging success, fledging weight, and weight of nestlings not fledged by last check[a] of Tufted Puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

	Buldir Island-1975		Ugaiushak Island-1976		Ugaiushak Island-1977	
	N	wt.(g)	N	wt.(g)	N	wt.(g)
Total number of nestlings monitored	2		50		21	
Nestlings fledged	0		19 (38%)		6(28.6%)	
$\bar{x}$				567.0		556.0
s				37.2		37.3
Max.				642.0		609.0
Min.				509.0		496.0
Nestlings of fledging weight[b] not fledged	0		21 (42%)		7(33.3%)	
$\bar{x}$				563.0		572.0
s				36.6		44.8
Max.				623.0		635.0
Min.				510.0		504.0
Nestlings below fledging weight not fledged	2 (100%)		3 (6.0%)		7(33.3%)	
$\bar{x}$		322.0		469.0		385.0
s		42.4		35.5		64.5
Max.		352.0		490.0		461.0
Min.		292		428.0		327.0
Nestling Mortality	0-100%		14.0-20.0%		4.8-38.1%	
Fledging Success	0-100%		80.0-86.0%		61.9-95.2%	

[a]1975=3 Sept.; 1976=2 Sept.; 1977=27-28 Aug.

[b]Fledging weight taken as 496 g, or approximately 64% of adult body weight (see text)

Tufted Puffins, generally, have been reported as having a high fledging success, averaging 60-70% in North America (Wehle, Chapter II, Table 47).

I have no information as to the causes of chick mortality observed in 1976 and 1977. Chicks were either found dead in their burrows or had disappeared. I observed no instances of predation on puffin nestlings. In other colonies, however, predation of Tufted Puffin nestlings by River Otters (Amaral 1977, Lehnhausen 1980) and Arctic Foxes (R. H. Day, pers. comm.) may significantly affect fledging success. Other reported causes of chick mortality in Tufted Puffins are weather related factors (Amaral 1977) and lack of food (Vermeer et al. 1979).

Estimated fledging success of Horned Puffins was 0-100% in 1975 on Buldir Island and 9-91% in 1977 on Ugaiushak Island (Table 16). Based on analysis of growth rates (see "Growth Rates of Nestlings"), the two Horned Puffin chicks on Buldir Island in 1975 grew significantly more slowly than chicks reported from any other colony. Thus, I doubt that either of these chicks successfully fledged (fledging success = 0%). On the other hand, growth rates of the 10 surviving chicks on Ugaiushak Island in 1977 were the highest reported from any colony; hence, all of these chicks probably fledged (fledging success = 91%). The average fledging success of Horned Puffins in 10 colony-years of study was 53-77% (Wehle, Chapter II, Table 48).

Cause of death for the single monitored Horned Puffin chick on Ugaiushak Island in 1977 was unknown. Death of this chick, as well as that of all chicks observed outside of the study plots, occurred at less than 2 weeks of age. I observed no instances of predation on

Table 16. Fledging success and weight of nestlings not fledged by last check[a] of Horned Puffins on Buldir Island, 1975, and Ugaiushak Island, 1977.

		Buldir Island-1975		Ugaiushak Island-1977	
		N	wt.(g)	N	wt.(g)
Total number of nestlings monitored		2		11	
Nestlings fledged		0		0	
Nestlings of fledging weight[b] not fledged		0		1(9.1%)	
	$\bar{x}$				403
	s				
	Max.				
	Min.				
Nestlings below fledging weight not fledged		2(100%)		9(90.9%)	
	$\bar{x}$		257.5		328.0
	s		29.0		59.2
	Max.		278.0		395.0
	Min.		237.0		238.0
Nestling mortality		0-100%		9.1-90.9%	
Fledging Success		0-100%		9.1-20.9%	

[a]1975=3 Sept.; 1977=28 Aug.

[b]Fledging weight taken as 400 g, or approximately 67% of adult body weight (see text).

Horned Puffin nestlings in any year. Predators of nestlings reported in other colonies have been River Otters (Amaral 1977) and Arctic Foxes (R. H. Day, pers. comm.). On east Amatuli Island, AK, Horned Puffin nestlings died as a result of flooded nest-sites caused by heavy rains and high surf (Amaral 1977).

BODY WEIGHT AND FAT CONTENT OF ADULTS DURING THE BREEDING SEASON

Body weight and fat content determinations were obtained from adult Tufted and Horned puffins collected for stomach content analysis at various phenological stages during the 1975 breeding season on Buldir Island.

Immediately after birds were collected, I weighed each bird to the nearest 1 g with a 1000 g Pesola spring balance. Sex was determined by dissection. Fat content of each bird was scored according to the following scheme modified from that of McCabe (1943):

1.	No Fat -	Hardly more than a hint in the dorsal tract or about the pygostyle.
2.	Little Fat -	A substantial depth in the dorsal tract, some fat in the furcula.
3.	Moderately Fat -	Quite heavy in the tracts, with small plates elsewhere in the skin. Crotch of the furcula fairly well filled.
4.	Fat -	Moderate sheets removable as such from many parts of skin.
5.	Very Fat -	Considerable amounts of solid fat inside the abdominal cavity, filling in between the intestinal folds, but the latter not hidden or embedded.

6. Excessively Fat - Deep sheets of fat everywhere between skin and muscle, even over the back. Intestines solidly embedded and overlaid, scarcely visible.

To detect possible variation in body weight and fat content during the breeding season, each bird was assigned to one of four breeding stages according to the following phenology:

Breeding Stage	COLLECTION DATES Tufted Puffin	Horned Puffin
Pre-egg	17 May - 2 June	28 May - 2 June
Egg	5 June - 25 July	5 June - 25 July
Early Nestling	11 Aug - 18 Aug	8 Aug - 11 Aug
Late Nestling	21 Aug	18 Aug - 21 Aug

Tests for significant differences in the mean body weight of adults between breeding stages were made using a Student's t-test at $p < 0.05$. As the index of the fat content was a subjective value. no statistical comparisons were made.

Tufted Puffin males showed a significant decrease in weight between the pre-egg stage and the early nestling stage, but showed a significant increase in weight between the early and late nestling stages (Table 17). They lost an average of 8.5% of their weight betwen first arrival at the colony and about midway in the nestling period, after which they regained an average of 2.5% of their pre-egg weight.

Mean body weights of Tufted Puffin females collected during each of the phenological periods indicated the same pattern of weight fluctu-

Table 17. Body weight and index of fat content of adult Tufted and Horned puffins at different phenological stages of the breeding period on Buldir Island, 1975.

	Body Weight (g)						Index of Fat Content					
	Male			Female			Male			Female		
	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s
Tufted Puffin												
Pre-egg Stage	9	806	30.7	6	758	44.3	9	4.2	0.97	5	4.2	0.45
Egg Stage	17	770	32.2	20	731	62.2	17	3.9	0.38	20	4.1	0.55
Early Nestling Stage	8	738	34.8	4	706	11.1	8	2.6	0.52	4	2.8	0.65
Late Nestling Stage	8	786	34.0	7	732	38.5	8	3.1	0.35	7	3.0	0.29
Horned Puffin												
Pre-egg Stage	3	475	17.8	5	486	22.2	3	4.7	0.58	4	4.5	0.58
Egg Stage	15	509	27.9	27	486	32.9	15	3.9	0.50	27	3.8	0.59
Early Nestling Stage	1	580	-	3	469	19.0	1	3.0	-	2	2.8	0.35
Late Nestling Stage	4	518	60.0	7	473	29.0	4	2.9	0.25	7	2.5	0.41

ation as males, but the difference between any two stages was not statistically significant, probably due to small sample sizes.

This pattern of initial weight loss followed by weight gain was also illustrated by the index of fat content (Table 17). Horned Puffin body weights showed no apparent fluctuation during the breeding season; however, fat content decreased continuously throughout the breeding season in both males and females. Similarly, in the northern Bering Sea region, Sealy (1973b) found that Horned Puffins lost less than 5% of their body weight throughout the breeding season.

Belopol'skii (1951) found that the body weight of Common Puffins, like Tufted Puffins, fluctuated considerably more (10.8%) than for Horned Puffins; however, unlike Tufted Puffins, Common Puffins continued to lose weight throughout the breeding season to August.

SUBADULTS

Subadult puffins, which can be distinguished from adults by differences in plumage and bill shape and color (Ridgway 1919, Dement'ev and Gladkov, 1951, Kozlova 1957), arrived at the breeding colony each year in July (Table 18) about 2.5 mo after the adults. They were present regularly throughout the rest of the breeding season, both in nearshore rafts and on the breeding colony. Subadult Tufted and Horned puffins were most frequent in areas not generally used by breeding puffins, i.e., on small cliff ledges.

In all years, the arrival of subadult Tufted Puffins coincided with a dramatic increase in the excavation of new burrows and the recon-

Table 18. Dates of first arrival of subadult Tufted and Horned puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

	Buldir Island	Ugaiushak Island	
	1975	1976	1977
Tufted Puffin	25 July	3 July	12 July
Horned Puffin	25 July	16 July	20 July

struction and cleaning of old, unused burrows. In general, adult puffins were not aggressive towards the subadults, which frequently trespassed their territorial boundaries.

Although both sexes were present (as evidenced from specimens collected), subadults present on the colony showed no indication of pairing.

PREDATION AND CLEPTOPARASITISM OF ADULTS

The major predators of adult puffins were Snowy Owls (Nyctacea scandiaca) on Buldir Island and Peregrine Falcons and Bald Eagles (Haliaeetus leucocephalus) on both Buldir and Ugaiushak islands. On the basis of carcasses found, Snowy Owls preyed much more heavily on Horned than Tufted puffins, probably because both Snowy Owls and Horned Puffins occupied the higher elevations of the island, where Tufted Puffins generally did not occur. Predation of puffins by Snowy Owls has also been reported on Aguttu Island, AK, (Williams and Frank 1979).

Predation of adult puffins by Peregrine Falcons was low on both islands, apparently due to the abundance of the smaller alcids and storm-petrels which were preferred by the falcons. Peregrine Falcons were observed to prey on both puffin species on the Barren Islands, AK; however, their overall impact on the population was minimal (Amaral 1977).

Bald Eagles on Buldir and Ugaiushak islands fed adult Tufted and Horned puffins to their nestlings. I examined the prey remains pre-

sent at one eagle eyrie each year. Prey remains were gathered twice during the summer in 1975, once in 1976, and 11 times in 1977. Collectively, puffins were the second most frequent prey in 1975 and 1976 and the most numerous in 1977 (Table 19). Puffins were probably also eaten by adult and subadult Bald Eagles, although I have no information as to the extent. While Bald Eagles probably took more puffins than any other predator, their impact on the puffin population was negligible on both islands. Predation of adult puffins by Bald Eagles in other colonies has been reported by Amaral (1977) and DeGange and Nelson (1978).

Elsewhere in their ranges, Tufted and Horned puffins are also preyed upon by Arctic and Red foxes (R. H. Day, pers. comm; J. L. Trapp, pers. comm.) and River Otters (Amaral 1977, Lehnhausen 1980). The major influence of these mammalian predators is not so much direct predation as a restriction of the puffins to more protected nest-sites.

Cleptoparasitism, the robbery or piracy of food being carried by puffins to their nestlings was minimal in all years. While both Glaucous-winged Gulls and Parasitic Jaegers (Stercorarius parasiticus) occurred on both islands, cleptoparasitism was observed by both species only a few times each year and had no significant effect on the success rate of feeding chicks. Cleptoparasitism of Tufted Puffins by Glaucous-winged Gulls on East Amatuli Island, AK, was also considered to have no significant effect on the feeding of chicks (Manuwal and Boersma 1978).

Table 19. The number and frequency of prey species remains found at Bald Eagle eyries on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

Prey Species	Buldir Island-1975		Ugaiushak Island-1976		Ugaiushak Island-1977	
	No.	%	No.	%	No.	%
Tufted Puffin (Lunda cirrhata)	4	14.8	4	12.5	1	1.7
Horned Puffin (Fratercula corniculata)	1	3.7	4	12.5	19	32.2
Unidentified Puffin			2	6.3		
Fork-Tailed Storm-Petrel (Oceanodroma furcata)	2	7.4				
Leach's Storm-Petrel (O. leucorhoa)	2	7.4				
Pelagic Cormorant (Phalacrocorax pelagicus)			1	3.1		
Undentified cormorant					1	1.7
Aleutian Canada Goose (Branta canadensis leucopareia)	1	3.7				
Parasitic Jaeger (Stercorarius parasiticus)	1	3.7				
Glaucous-winged Gull (Larus glaucescens)	1	3.7			1	1.7
Black-legged Kittiwake (Rissa tridactyla)	1	3.7			3	5.1
Common Murre (Uria aalge)			15	46.9	5	8.5
Thick-billed Murre (U. lomvia)			2	6.3	5	8.5
Unidentified murre					13	22.0
Pigeon Guillemot (Cepphus columba)	1	3.7	1	3.1	1	1.7

FEEDING OF ADULTS

Tufted and Horned puffins capture their prey by pursuit diving in which a bird on the surface dives and pursues its prey underwater (Ashmole 1971). Like other alcids, puffins swallow their prey underwater. Puffins generally feed singly but sometimes also feed in monospecific and mixed species assemblages (Sealy 1973c, Moe and Day 1979, Sanger et al. 1978,). There is currently no reliable information on the depths at which puffins feed; however, seabirds, including Tufted and Horned puffins, are frequently found entangled in the upper one-third of 6 m deep Japanese drift gill nets (DeGange 1978).

In the following discussion, the foraging habitats used by Tufted and Horned puffins are described as a combination of the distance from shore and the depth of water in which the species feed; they consist of three main types, after Day (1980):

1. Inshore Waters: waters less than 40-50 m deep and usually within sight of land;

2. Offshore Waters: waters of the continental shelf extending from 40-50 m in depth seaward to and including the shelf break, and usually out of sight of land;

3. Oceanic Waters: waters extending from the shelf break to the deep waters of the open ocean, and almost always out of sight of land.

The foraging habitat used by Tufted Puffins varies considerably within a single breeding season at the same colony and between colonies. On Buldir Island, Tufted Puffins fed in offshore or oceanic waters until the beginning of the nestling period, after which they

foraged primarily in inshore waters (Wehle 1976). This same pattern was also observed in the Kodiak Island area in 1977 (Sanger et al. 1977). Tufted Puffins fed in inshore waters around Ugaiushak Island throughout the 1976 and 1977 breeding seasons and have been reported feeding in inshore waters at least during the nestling period, around Kodiak Island in 1975 (Dick et al. 1976), Triangle Island, B.C. (Vermeer et al. 1979) and the Olympia Peninsula, WA, (Cody 1973). In the Shumagin Islands, AK, and on St. Lawrence Island, AK, Tufted Puffins were observed feeding primarily in offshore waters (Moe and Day 1979, Sealy 1973b, respectively). Based on the type of food brought to their young, Tufted Puffins on Middleton Islands, AK, were thought to forage beyond the continental shelf in oceanic waters (Hatch et al. 1979).

In contrast to Tufted Puffins, Horned Puffins exhibit little variation in their foraging habits. Horned Puffins on Buldir Island and Ugaiushak Island fed in inshore waters, usually within 1-2 km from shore, throughout the breeding season each year. This species has also been reported feeding primarily in inshore waters around Forrester Island, AK, (Willett 1915), the Shumagin Islands (Moe and Day 1979), St. Lawrence Island (Sealy 1973b) and the Pribilof Islands (Hunt et al., in prep.).

Since there is considerable overlap between Tufted and Horned puffins in the major prey types eaten (see below), the observed variation in foraging habitats of Tufted Puffins may reflect a form of ecological segregation between the two species related to food availability. During periods when food is abundant, both species may forage in

inshore waters, but during periods of food shortage, competition may be reduced by Tufted Puffins feeding further offshore than Horned Puffins. Thus, the concept of species specific foraging distances as a mechanism of ecological segregation proposed by Cody (1973) is probably more flexible in terms of when it occurs and less specifically defined in terms of actual distance than Cody indicated.

FOOD OF ADULTS AND SUBADULTS

To determine the major types of prey taken by adult and subadult Tufted and Horned puffins during the breeding season, I collected birds of both species during each of my three summer field seasons. In the following discussion, the results obtained from these collections are compared with other information on the diets of Tufted and Horned puffins.

Methods

Birds were obtained by shooting, either from the nearshore waters of the breeding colonies or on-shore. Once collected, each bird was injected with 25 cc of a 10% buffered formalin solution through the buccal cavity into the esophagus to retard digestion. The buccal cavity was then stuffed with cotton to prevent leakage of contents. Later, the digestive tracts from the anterior end of the esophagus to the beginning of the small intestine (hereafter, collectively referred to as the "stomach") were removed, opened, and placed

in vials containing a 10% buffered formalin solution for subsequent examination.

I analyzed contents of birds collected in 1975 and assigned them to four major categories: fish, squid, polychaetes, and plastic. Contents of birds collected in 1976 and 1977 were analyzed by the staff of the U.S. Fish and Wildlife Service, Office of Biological Services--Coastal Ecosystems, Anchorage, Alaska. Contents of these stomachs were assigned to 9 major prey types listed in Tables 20-21. Identification of individual prey species was made when prey items were in relatively good condition.

Results

Fish remains were primarily vertebrae, though partially digested whole fish remained in a few instances. Only the beaks and occasionally a broken radula remained in the stomachs as evidence of ingested squid. Similarly, only the paragnaths of polychaetes withstood immediate digestion in the stomach. The remains of ingested crabs and chitons consisted primarily of shell fragments. In some instances, shrimp, amphipods, euphausiids, and ticks were found in the esophagus in good enough condition to allow identification to species. In other cases, only digested organic matter remained. Plastic particles occurred in a wide range of colors, shapes, and sizes, with those from birds collected in 1975 measuring from less than 1.0 mm to approximately 14.0 mm at the longest dimension.

Table 20. Number and frequency of prey types in Tufted Puffin stomachs containing food items other than plastic alone (N), on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

	Buldir Island 1975 adults (N=73)		Buldir Island 1975 subadults (N=13)		Ugaiushak Island 1976 adults (N=14)		Ugaiushak Island 1977 adults N=6)	
Prey Type	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency %)
Fish	18	24.7	4	30.8	2	14.3	4	66.7
Squid	71	97.3	13	100	5	35.7	1	16.7
Polychaetes	1	1.4	3	23.1				
Crabs					3	21.4		
Shrimp							1	16.7
Euphausiids							2	33.3
Ticks					1	7.1		
Organics					2	14.3	1	16.7
Plastic	10	13.7	8	61.5	2	14.3	1	16.7

Table 21. Number and frequency of prey types in Horned Puffin stomachs containing food items other than plastic alone (N), on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

	Buldir Island 1975 adults (N=41)		Buldir Island 1975 subadults (N=6)		Ugaiushak Island 1976 adults (N=8)		Ugaiushak Island 1977 adults N=4)	
Prey Type	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)
Fish	11	26.8	3	50.0	2	25.0	3	75.0
Squid	36	87.8	4	66.7				
Polychaetes	3	7.3	2	33.3	1	12.5		
Chitons							1	25.0
Amphipods					1	12.5		
Organics					6	75.0	1	25.0
Plastic	20	48.8	2	33.3				

In 1975, almost all adult Tufted and Horned puffins which had food other than plastic in their stomachs contained squid remains; and approximately 25% of each species had evidence of ingested fish (Tables 20-21). Relatively few stomachs of either species contained polychaete remains, although they were slightly more common in Horned than Tufted puffins.

In 1976, squid, crab, and fish, respectively, were the most common prey remains found in Tufted Puffin stomachs. In contrast, none of the Horned Puffin stomachs examined in 1976 contained squid or crab remains and only 25% contained fish remains; the majority contained unidentified organic matter. The presence of 10 ticks found in the stomach of one Tufted Puffin collected in 1976 was probably the result of ingestion during preening.

The majority of Tufted and Horned puffin stomachs examined in 1977 contained fish remains. Euphausiids, shrimp, and squid were present in a small number of Tufted Puffin stomachs but not in those of Horned Puffins. A single Horned Puffin stomach contained shell fragments of a chiton, a prey item not found in Tufted Puffin stomachs.

Although the great variation in sample sizes between adults and immatures dictates caution in making comparisons between age classes, the data indicate that relatively more immature Tufted and Horned puffins ingested fish and polychaetes than did adults (Tables 20-21). The incidence of ingested squid was similar between age classes of Tufted Puffins and slightly lower in immature than adult Horned Puffins.

The frequency of prey items found in the stomachs of immature Tufted and Horned puffins indicates that more immature Tufted Puffins fed on squid than did immature Horned Puffins, while a relatively greater proportion of immature Horned Puffins fed on both fish and polychaetes than did immature Tufted Puffins.

Analysis of food types present in the stomachs of adults collected at different stages of the breeding period on Buldir Island (Table 22) shows that, for Tufted Puffins, the frequency of squid remained high through all breeding stages, whereas for Horned Puffins, the frequency of squid decreased from an average of 96% during the pre-egg and egg stage to 67% during the nestling stage. Polychaetes were evident only in the pre-egg stage for Tufted Puffins, while they appeared only during the incubation and hatching stages for Horned Puffins. For both Tufted and Horned puffins the frequency of fish was highest during the nestling stage.

During each of the 3 years, a number of collected Tufted and Horned puffins contained plastic particles in their stomachs (Table 23). Of the 228 stomachs examined, 60 (26.3%) contained at least one piece of plastic. Both Tufted and Horned puffins on Buldir Island showed a higher incidence of plastic in their stomachs than did either species during both years combined on Ugaiushak Island. On Buldir Island, the frequency of plastic in stomachs was over three times greater for adult Horned Puffins (47.7%) than for adult Tufted Puffins (15.1%); however, 7 of 13 immature Tufted Puffins had plastic in their stomachs compared with 3 of the 8 immature Horned Puffins. Throughout the breeding season, the frequency of plastic in the stomachs of Tufted

Table 22. Number and frequency of puffin stomachs containing fish, squid and polychaetes at different stages of the breeding period, based on stomachs containing food items other than plastic alone (N), for adult Tufted and Horned puffins on Buldir Island, 1975.

	N	FISH		SQUID		POLYCHAETES	
		No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)
Tufted Puffin							
Pre-egg Stage	14	5	35.7	13	92.9	1	7.1
Egg Stage	32	2	6.3	32	100	0	0.0
Nestling Stage	27	11	40.7	26	96.3	0	0.0
Horned Puffin							
Pre-egg Stage	3	0	0.0	3	100.0	0	0.0
Egg Stage	27	5	18.5	25	92.6	3	11.1
Nestling Stage	12	6	50.0	8	66.7	0	0.0

Table 23. Number and frequency of puffin stomachs containing plastic, based on all stomachs examined (N) for Tufted and Horned puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

		N	No.	Frequency (%)
Tufted Puffin				
Adult:	1975	86	13	15.1
	1976	28	1	3.6
	1977	6	1	16.7
Subadult:	1975	13	8	61.5
	1976	2	1	50.0
Horned Puffin				
Adult:	1975	65	31	47.7
	1976	14	1	7.1
	1977	6	1	16.7
Subadult:	1975	8	3	37.5

Puffins was the highest during the egg stage but remained relatively consistent in Horned Puffins (Table 24).

Discussion

Almost all remains found in the stomachs (fish vertebrae, squid beaks, polychaete paraganths, shell fragments and plastic) were either not digestible or were being digested at a slow rate. The length of time these "hard parts" remain in the stomachs of puffins after initial ingestion is not known. For plastic, Day (1980) estimated the residence time of "soft" and "hard" polyethylene to be 2-3 mo and 12-15 mo, respectively. It is possible that some hard parts may be from items taken in wintering areas or during spring migration and not during the breeding season. If the residence time of these hard parts in stomachs was less than 2-3 mo, then stomach contents of adults collected during the nestling period would more correctly reflect prey items taken during the breeding season than birds collected earlier. Data from birds collected in 1975, however, indicate that the frequency of squid remained high throughout the breeding season in Tufted Puffins and dropped only slightly during the nestling period in Horned Puffins (Table 22). The occurrence of fish, on the other hand, was more variable throughout the breeding season, but both species showed the highest frequency during the nestling stage. The increase in the frequency of fish during the nestling period is probably the result of fish shoaling near the island at that time. Further, both species were observed carrying fish and squid to their nestlings (see below), so it

Table 24. Number and frequency of stomachs containing plastic at different stages of the breeding period, based on the total number of stomachs examined during that period (N), for adult Tufted and Horned puffins on Buldir Island, 1975.

	N	No.	Frequency (%)
Tufted Puffin			
Pre-egg Stage	16	1	6.3
Egg Stage	42	10	23.8
Nestling Stage	28	2	7.1
Horned Puffin			
Pre-egg Stage	8	4	50.0
Egg Stage	43	21	48.8
Nestling Stage	14	5	35.7

is likely that adults also consumed these prey types during the nestling period. Immature Tufted and Horned puffins were collected shortly after their arrival in July, and, hence, it is likely that hard parts present in the stomachs of these birds represented prey items taken prior to the birds' arrival to the water around the breeding colony.

Data in Tables 25 and 26 indicate that fish are usually the predominant prey item taken by both puffin species. Exceptions were on Buldir Island, where the frequency of squid in Tufted and Horned puffins was at least three times greater than that of fish, and on Ugaiushak Island where both fish and squid were present in equal numbers in Tufted Puffins. These data probably exaggerate the importance of fish and squid in the diets of Tufted and Horned puffins; while the importance of soft-bodied organisms without "hard parts" (primarily crustaceans) is probably underestimated because of differences in the digestion rate of different prey (Hartley 1948, Goss-Custard 1969, Swanson and Bartonek 1970, Custer and Pitelka 1975).

The predominant prey species of fish taken by Tufted and Horned puffins varied between colonies and between puffin species at the same colony. On the Pribilof Islands, Walleye Pollock (Theragra chalcogramma) represented almost half of the fish taken by Tufted Puffins while in the Kodiak Island area osmeriids, primarily Capelin (Mallotus villosus), had the highest frequency-of-occurrence in Tufted Puffins. Relatively fewer Horned than Tufted Puffins on the Pribilof Islands fed

Table 25. Number and frequency of prey types in the stomachs of adult Tufted Puffins.

	Alaskan Waters 1969-1976 all seasons (N=34)		Pribilof Islands, AK 1975-1978 summer (N=23)		Buldir Island, AK 1975 summer (N=76)		Ugaiushak Island, AK 1976-1977 summer (N=20)		Kodiak Island Area, AK 1977 summer (N=89)	
Prey Type	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)
Fish	20	58.8			18	23.7	6	30.0	85	95.5
Ammodytidae									2	2.2
Osmeridae			1	4.4					65	73.0
Gadidae			14	60.9					8	9.0
Cehpalopoda	18	52.9	2	8.7	71	93.4	6	30.0	12	13.5
Crustacea	4	11.8	1	4.4						
Amphipoda			2	8.7						
Decapoda							4	20.0		
Euphausiacea							2	10.0	6	6.7
Polychaeta			6	26.1	1	1.4			1	1.1
Other							4	20.0		
Sources	Sanger and Baird (1977)		Hunt et al. (in prep.)		this study		this study		Sanger et al. (1978)	

Table 26. Number and frequency of prey types in the stomachs of adult Horned Puffins.

	Alaskan Waters 1969-1976 all seasons (N=14)		Cape Thompson AK 1959-1961 summer (N=8)		Pribilof Islands 1975-1978 summer (N=39)		Buldir Island 1975 summer (N=52)		Ugalushak Island 1976-1977 summer (N=12)	
Prey Type	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)	No.	Frequency (%)
Fish	11	78.6	6	75.0			11	21.2	5	41.7
Ammodytidae			2-3	25.0-37.5	6	15.4				
Hexagrammidae					8	20.5				
Osmeridae			1	12.5	1	2.6				
Gadidae			3-4	37.5-50.0	12	30.8				
Trichodontidae					4	10.3				
Cottidae			1	12.5						
Cehpalopoda	2	14.3			4	10.3	36	69.2		
Other Mollusca									1	8.3
Crustacea	4	28.6	1	12.5	3	7.7				
Amphipoda					2	5.1			1	8.3
Decapoda										
Polychaeta			2	25.0	10	25.6	3	5.8	1	8.3
Porifera			1	12.5						
Other									7	58.3
Sources	Sanger and Baird (1977)		Swartz (1966)		Hunt et al. (in prep.)		this study		this study	

on Walleye Pollock, but Horned Puffins consumed three inshore subtidal species not taken by Tufted Puffins; Pacific Sand Lance (Ammodytes hexapterus), Whitespotted Greenling (Hexagrammos stelleri), and Pacific Sandfish (Trichodon trichodon). Horned Puffins at Cape Thompson, however, took primarily Arctic Cod (Boreogadus saida) and Pacific Sand Lance.

The diets of Tufted and Horned puffins also show seasonal variation within the summer breeding period. The nature of this seasonal variation depends on the geographic area. For example, both Tufted and Horned puffins on Buldir Island showed an increase in the frequency of fish during the nestling period and in Horned Puffins a concommitant decrease in the frequency of squid during this period. In the Kodiak Island area, the frequency of fish, and to some extent squid, decreased in Tufted Puffins during the nestling period while the frequency of euphausiids and polychaetes increased. The decrease in total fish consumption corresponded to an increase in the number of fish species taken, with sand lance and Walleye Pollock supplementing Capelin--which were taken almost exclusively earlier in the breeding season.

Thus, both Tufted and Horned puffins exhibit seasonal, yearly, and geographic variation in their diets. Although fish are the major prey item taken by both species, Horned Puffins appear to take a greater variety of fish, especially inshore, subtidal species, than do Tufted Puffins. On the other hand, Tufted Puffins more regularly supplement their diet with squid than do Horned Puffins. However, despite these general preferences, both species appear to be flexible

in their preferences of diet and are opportunistic in taking advantage of locally or temporarily abundant prey types.

The occurrence of plastic in the stomachs of puffins and other seabirds in Alaskan waters has been discussed by Day (1980). Based in part on stomach samples reported in this study, he found the incidence of plastic in birds collected in the Aleutian Islands greater than in birds collected in the Gulf of Alaska or in the Bering and Chukchi seas. These geographic differences may be explained in terms of non-uniform geographic input of plastic and subsequent dispersal by currents. The source of the plastic found in Alaskan seabirds includes at-sea dumping of wastes by fish and cargo boats, effluents from plastic-manufacturing plants, and the loss from ships transporting plastic material. The cause of plastic ingestion by puffins and other seabirds is probably due to mistaken identity, in that the plastic resembles food items typically eaten by the birds (Day 1980). Although the data are limited, Day (1980) found no overt effects of plastic ingestion on the physical quality of birds examined.

FEEDING, FOOD, AND GROWTH OF NESTLINGS

The purpose of this section is threefold: 1) to report the results of this study on the feeding, food, and growth of Tufted and Horned puffin nestlings, 2) to compare these results with those of similar studies, and 3) to correlate the information for (1) and (2) above with the observed variation in breeding success reported earlier for different colony-years of the two puffin species.

Methods

Bill loads of food carried by Tufted and Horned puffins in 1975 were collected primarily by placing mist nets over nest-site entrances. Upon landing, birds became entangled in the nets and dropped their bill loads which I subsequently collected. A few food-carrying birds were collected by shotgun. Using these two methods, I collected 15 bill loads each of Tufted and Horned puffins between 14 and 21 August.

Loads carried by Tufted Puffins in 1976 and 1977 were collected from marked burrows affixed with an observation hole into the nest chamber as described above. From within a blind, I could observe when an adult bird carrying food landed on the colony and entered one of these burrows. When this occurred, I immediately left the blind and opened the observation hole of the burrow and collected the food sample. Using this technique, I collected 41 complete bill loads between 3 and 31 August, 1976 and 31 complete loads between 10 and 27 August, 1977.

For each sample collected in 1975-1977, I counted the number of prey per load, measured the total weight of the load to the nearest 0.5 g, and measured the total length of individual prey to the nearest 0.5 mm. Total lengths of fish were measured from the tip of the snout to the tip of the tail, and of squid from the anterior end of the mantle to the tip of the longest tentacle. Bill loads were stored in a 10% buffered formalin solution, and individual prey items were later identified by me or by members of the staff of the Aquatic Collections, University of Alaska Museum, Fairbanks.

In addition to the collection of actual bill loads described above, I was also able to determine the prey-type and number for 33 other bill loads using 10 x 50 binoculars from within the blind. Identification of individual prey species was possible in all cases except for Walleye Pollock (Theragra chalcogramma) and Saffron Cod (Eleginus gracilis), which could not be reliably distinguished at a distance. Hence, these two species are lumped together in the following analysis.

The nature of the nesting habitat used by Horned Puffins on Ugaiushak Island precluded the use of the same techniques to recover prey items. Information on food carried to Horned Puffin chicks comes from partial bill loads found within the colony and from general observations.

During this study I measured the growth rates of Tufted and Horned puffin chicks raised under natural conditions and under a variety of experimental situations (Table 27), to assess the relative quantity and/or quality of food available to chicks each year. "Unfed singles" were chicks raised by their parents in their natural nesting habitat (this is the normal or natural situation); "unfed twins" were artificially twinned chicks (chicks twinned by adding a chick from one nest-site to a nest-site containing another chick of nearly equal weight or age) raised and fed by the parents of one of the chicks in its natural nesting habitat; "fed singles" and "fed twins" were chicks that were raised by one of the chick's parents in its natural habitat and which received an additional supplement of food from me; and "captive singles" and "captive twins" were chicks that were held in captivity and fed only by me.

Table 27. The number of Tufted and Horned puffin chicks in natural and experimental situations for which growth rates were measured on Buldir Island, 1976, and Ugaiushak Island, 1976 and 1977.

Year	Situation[a]	Tufted Puffin	Horned Puffin
1975	Unfed singles	2	2
	Captive singles	1	0
1976	Unfed singles	27	0
	Unfed twins	1 (4)[b] pair	0
1977	Unfed singles	10	10
	Fed singles	5	4
	Unfed twins	3 (6) pair	3 (4) pair
	Fed twins	7 (11) pair	1 (3) pair
	Captive singles	1	2
	Captive twins	0	1 pair

[a]For explanation of situations, see text.

[b]Numbers in parentheses indicate the initial number of pairs twinned; however, due to death, desertion, or other factors, growth rates were not obtained from all the original pairs of twins.

Comparisons of growth rate for chicks reared under different situations are based on the weight gain per day of chicks during the interval from age 5-25 days. Total weight of chicks was measured to the nearest 0.5 g for chicks under 100 g, and to the nearest 1 g as the chicks grew over 100 g. Weights were taken daily on Buldir Island, weather permitting, and at 1-5 day intervals (usually every second or third day) on Ugaiushak Island, depending on weather and the location of study plots on the island.

All captive chicks were taken from their nest-sites when adults terminated brooding, and were raised in dark wooden enclosures kept at a relatively cool and constant environmental temperature. Captive chicks were provided with as much food as they would eat at least twice daily. Food for the captive Tufted Puffin chick on Buldir Island consisted primarily of partially digested fish dropped or regurgitated by Glaucous-winged Gull chicks. In a few instances when this source of food was not available, the chick's diet was supplemented with canned salmon, tuna, and/or sardines. Captive chicks on Ugaiushak Island were fed primarily small fresh filets of Black Rockfish (Sebastes melanops), but were also given a variety of whole fresh fish (sand lance, Capelin, Walleye Pollock, Saffron Cod, Chum Salmon (Oncorhynchus keta), and Pacific Herring (Clupea harengus) collected from bill loads of Tufted Puffins or found around the seabird breeding colonies. This diet was supplemented with a commercial brand multi-vitamin and multi-mineral supplement.

Chicks in all sets of twins for which growth rates were measured were twinned when less than 2 days old.

Fed singles and fed twins were given a food supplement consisting of filets of Black Rockfish and small whole fish obtained from the sources mentioned above. Fed singles of both Tufted and Horned puffins received 50 g of this food supplement once daily beginning when the chicks were 3 days old. Fed twins of both species together received 50 g of food once daily when 3 to 7 days old, and 100 g of food once daily thereafter. Supplemental food was placed at the entrance to the nest chamber for Tufted Puffins and near the actual nest for Horned Puffins.

Variations in the growth rates of chicks were compared using a covariance analysis for the linear portion of the growth curve. The linear portion of the normal sigmoid growth curve for body weight plotted against the chick's age in days, was determined for Tufted and Horned puffins using a least squares polynomial curve fit analysis for 10 chicks of each species raised under natural conditions. From the regression line thus obtained growth proceeded in a nearly linear fashion from day 5 to day 30 in both species. The mean rates of growth for chicks reared under different conditions in this study and for chicks in other studies were calculated and their differences compared by analysis of covariance. Growth rates were considered significantly different if the F-value obtained by analysis of covariance was equal to or exceeded the critical values of the F-distribution at $p < 0.05$.

Results and Discussion

Delivery of Food

The method of food transfer from adult to chick has not been previously described for Tufted or Horned puffins. In 1977, I witnessed the first food delivery to two Horned Puffin chicks. Each chick was less than 1 day old when it was brought its first meal. At the time of my observations, both chicks were being brooded by one adult when the other adult entered the nest-site carrying food. In both instances, the bill load of food consisted of two sand lance approximately 60 mm long. In one case, the food-carrying adult entered the nest-site and immediately dropped the food on the floor near the nest containing the brooding adult and chick. At this point, the food-carrying adult saw me and flushed from the rock crevice. Shortly thereafter, the chick emerged from under the brooding adult and began walking around the nest, alternately picking up and dropping bits of vegetation with its bill. Finally, it picked up one of the sand lance, and swallowed it head first. This was immediately repeated with the second fish. The chick then proceeded to pick up and drop additional pieces of vegetation before returning to the attending adult.

In the second case, after the food carrying adult Horned Puffin entered the nest-site and dropped the fish near the nest, the bird lowered its head and moved it slowly from side to side while uttering a faint low-pitched "errr" sound. This bird then left the nest-site. Almost immediately thereafter, the chick emerged from the brooding

adult, walked directly over to the two fish and immediately ate one after the other, swallowing them head first. From these two observations, it appears that the method of transfer of food from adult to chick is not direct, but involves the fish first being dropped on the floor of the nest-site and then being picked up and eaten by the chick. The second observation also suggests that particular vocalizations and/or behavior of the food-delivering adult may cue the chick to the presence of food.

Although I never observed an adult Tufted Puffin arrive with the first load of food for its chick, on several occasions I observed one or two small sand lance lying on the floor of a burrow near a brooding adult and chick. Presumably, in each instance, I arrived shortly after the departure of the food-delivering adult.

As the chicks of both species grew older, it became apparent that the adults dropped the food farther from the actual nest within the nest-site. Most of the bill loads collected from Tufted Puffins had been dropped at the entrance to the nest-chamber. As the time spent delivering food is typically very short in both species, I suspect that any cueing behavior to the chick as an indication that food is present is probably discontinued at the time brooding is terminated. Within a day or so after hatching, both Tufted and Horned puffin chicks made a peeping sound which became particularly acute when an adult carrying food entered the nest-site. Once the chicks had eaten, the vocalizations either ceased or became greatly reduced in intensity. Such vocalizations by chicks may stimulate the adults to bring them food.

In both Tufted and Horned puffins, males and females shared in feeding the young, but the degree of participation of the two sexes is unknown. As noted above, at least one of the adults broods the chicks for at least 1 day in Tufted Puffins and 5-7 days in Horned Puffins. During this period, the nonbrooding adult brings food to the chick. Whether there is an alternation of the adults between these two duties is unclear.

Feeding Frequency

Food deliveries to Tufted and Horned puffin chicks tend to occur in peaks. Typically, in the earlier stages of the nestling period, there are two peak activity periods per day, one in early to mid-morning and the other in late afternoon to early evening. In the later stages of the nestling period, there are usually three peaks of feeding activity per day, one in early to mid-morning, one in mid-afternoon and another just prior to nightfall (Amaral 1977, Baird and Moe 1978, Vermeer et al. 1979, this study).

There is considerable variation in the rate at which Tufted and Horned puffins feed their young (Table 28). In general, older chicks of both species receive a greater number of bill loads of food per day than do younger chicks (Amaral 1977). Presumably this rate increase is in response to the increasingly greater energy demands of the older chicks.

Baird and Moe (1978) taped the bills closed in 30 Tufted Puffin chicks (aged 19-40 days) for 24 h and 12 chicks for 48 h. On the

Table 28. Number of bill loads delivered to Tufted and Horned puffin nestlings per day.

Location	Year	Age of Chick	No. Loads/Day Mean	Range	Source
Tufted Puffin					
Triangle I., B.C.	1976			0-6	Vermeer et al. (1979)
Barren Is., AK	1976	1-7 days	1.6		Amaral (1977)
		4-6 weeks	3.8	2-6	Amaral (1977)
Horned Puffin					
Barren Is., AK	1976	3-8 days	1.0		Amaral (1977)
		12-17 days	2.5	2-3	Amaral (1977)
	1977		3.3	2-6	Manuwal and Boersma (1978)

basis of the presence or absence of food in the nest chamber at the end of these time periods, these authors found that an average of 21.4% of the chicks were not fed in a 24 h period and 8.3% were not fed in a 48 h period. I suggest, however, the presence of a "muzzle" on the chicks may have biased the results in at least two ways. First, the muzzle may have interfered with the chick's normal behavior. For instance, if adults are stimulated to feed the chick by the vocalizations of the chick, the muzzle may have inhibited such vocalizations and reduced the feeding initiative of the adults. The frequent vocalizations of both Tufted and Horned puffin chicks when being fed (see above) suggests that such a stimulus may exist. Second, adults may have consumed the food left untouched by the chicks. Both of these influences were presumed operating in another feeding study in which Tufted Puffin chicks were muzzled (Hatch et al. 1979).

Weather appears to exert only a minor influence on the feeding of puffin chicks. During each of the three years of my investigation, both Tufted and Horned puffins delivered food to their nestlings even under relatively adverse conditions. The only days when puffins did not regularly feed young were when seas were over 2 m, winds were greater than 40 knots, and when there was heavy precipitation. Nevertheless, even under these conditions, an occasional bird still made a food delivery.

Size and Weight of Food Loads

The number of prey items delivered per bill load by both Tufted and Horned puffins shows marked variation between colonies and between years at the same colony (Table 29). The number of prey per load does not vary consistently during the nestling period. On the Barren Islands in 1976, the average size of Tufted Puffin bill loads increased significantly from 1.3 to 3.8 prey items during the nestling period (Amaral 1977), while on Ugaiushak Island in 1977, the average size of Tufted Puffin bill loads decreased significantly during the nestling period from 6.2 to 4.2 prey items (this study). A similar decrease was observed on Triangle Island, B.C., in 1977 (Vermeer et al. 1979). In contrast, there was no significant change in the size of Tufted Puffin bill loads on Chowiet Island or Ugaiushak Island in 1976 (G. Burrell, pers. comm.; this study) nor for Horned Puffins on the Barren Islands or Chowiet Island in 1976 (Amaral 1977; G. Burrell, pers. comm.) Both Tufted and Horned puffins generally deliver 10-20 g of food per bill load (Table 30). During this study, there was no significant difference in the weight of loads delivered by Tufted Puffins in each of these three years. For the three colonies in which the weights of Tufted and Horned puffin bill loads were measured in the same year, there was also no significant difference between the two species in each year (Manuwal and Boersma 1978; G. Burrell, pers. comm.; this study).

As with load size, there does not appear to be a trend in the weight of bill loads delivered throughout the nestling period. For

Table 29. Number of prey items per bill load delivered to Tufted and Horned Puffin nestlings.

Location	Year	N	No. Prey/Bill Load Mean	Range	Source
Tufted Puffin					
Olympic Peninsula, WA		12	6.7	1-29	Cody (1973)
Buldir I., AK	1975	15	4.3	1-15	this study
Chowiet I., AK	1976	12	10.1	5-18	G. Burrell (pers. comm.)
Ugaiushak I., AK	1976	41	9.4	1-22	this study
	1977	64	5.6	1-13	this study
Barren Is., AK	1976	79	3.8	1-8	Manuwal and Boersma (1977)
	1977	58	3.4	1-8	Manuwal and Boresma (1977)
Horned Puffin					
Buldir I., AK	1975	15	3.5	1-11	this study
Shumagin Is., AK	1976	18	6.0	1-16	Moe and Day (1979)
Chowiet I., AK	1976	19	12.6	2-65	G. Burrell (pers. comm.)
Barren Is., AK	1976	26	1.5	1-3	Manuwal and Boersma (1978)
	1977	20	3.2	1-7	Manuwal and Boersma (1978)

Table 30. Weight (grams) of bill loads delivered to Tufted and Horned puffin nestlings.

Location	Year	N	Weight of Bill Loads Mean	Range	Source
Tufted Puffins					
Olympic Peninsula, WA		7	13.3		Cody (1973)
Triangle I., B.C.	1976				Vermeer et al (1979)
4-5 August		7	18.7		
23-31 August		9	13.0		
2-5 September		6	9.7		
Buldir I., AK	1975	13	11.9	4.9-24.4	this study
Chowiet I., AK	1976	12	7.5	2.3-16.8	G. Burrell (pers. comm.)
Ugaiushak I., AK	1976	41	9.7	2.5-27.8	this study
	1977	31	14.4	5.0-34.0	this study
Sitkalidak I., AK	1977	10	19.3	13.5-35.0	R. A. Moe (pers. comm.)
Barren Is., AK	1976	24	14.9	2.0-36.5	Manuwal and Boersma (1978)
	1977	28	20.4	9.0-35.0	Manuwal and Boersma (1978)
Horned Puffins					
Buldir I., AK	1975	15	11.0	5.5-15.7	this study
Shumagin Is., AK	1976		13.8	7.4-25.4	Moe and Day (1979)
Chowiet I., AK	1976	19	7.9	2.5-19.0	G. Burrell (pers. comm.)
Barren Is., AK	1976	9	10.7	3.0-19.0	Manuwal and Boersma (1978)
	1977	13	17.0	3.0-35.0	Manuwal and Boersma (1978)

Tufted Puffins, Cody (1973) and G. Burrell (pers. comm.) noted an insignificant increase in load weight during the nestling period while Vermeer et al. (1979) observed a gradual decrease in the average weight per load throughout this period. Similarly, Baird and Moe (1978) found a significant decrease in the total weight of food delivered per day to Tufted Puffin chicks as they grew older. Chicks 19-30 days old received a mean of 28.9 g/day (s 37.8) while chicks 31-40 days old received only 15.9 g/day (s 12.1). On Ugaiushak Island, there was no significant difference in the weight of bill loads delivered between early and late August in either 1976 or 1977.

For Horned Puffins, G. Burrell (pers. comm.) found a significant increase in load weight delivered to chicks during the nestling period on Chowiet Island in 1976. No other information on load weights of this species is available.

Species Composition of Food Loads

Data on the frequency of individual prey species delivered to Tufted and Horned puffin nestlings during 11 colony-years of study for both species indicate that either Pacific Sand Lance or Capelin was the most numerous prey species delivered during each colony-year (Tables 31-32). In Tufted Puffins, sand lance and/or Capelin comprised over 90% of all prey items delivered in five of the seven colony-years, and in Horned Puffins, these two species of fish accounted for over 85% of all prey items delivered in three of the four colony-years. In each of the three colony-years not following this pattern, sand

Table 31. Number and percent of individual prey items of different species delivered to Tufted Puffin nestlings.

	Buldir Island 1975		Ugaiushak Island 1976		Ugaiushak Island 1977		Sitkalidak Island 1977		Barren Islands 1976		Barren Islands 1977		Middleton Island 1978	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Oncorhyncus keta-Chum Salmon					2	0.5								
O. nerka-Sockeye Salmon							5	1.6						
Mallotus villosus-Capelin			11	2.6	42	13.0	215	64.9	104	94.5	86	57.0		
Theragra chalcogramma-Walleye Pollock			14	3.4	17[a]	4.9[a]	12	3.7						
Eleginus gracilis Saffron Cod			12	2.9										
Gadus macrocephalus-Pacific Cod											9	6.0		
Trichodon trichodon-(Pacific) Sandfish							11	3.1			1	0.7	1	1.5
Lumpenus sp.			1	0.2										
Zaprora silenus-Prowfish	1	1.6							2	1.8			2	3.1
Ammodytes hexapterus-Pacific Sand Lance	23	36.5	370	88.8	287	82.0	86	25.8			46	30.3	39	60.0
Sebastes sp.			1	0.2										
Pleurogrammus monopteryglus-Akta Mackeral	4	6.3												
Hexagrammos decagrammus-Kelp Greenling											4	3.0		
Hemilepidotus jordani	13	20.6												
Aspidophoroides bartoni	1	1.6												
Cephalopoda	21	33.3			1	0.3	1	0.3	4	3.6	4	3.0	10	15.4
Octopoda					1	0.3	2	0.6					13	20.0
Crustacea			8	1.9										
Source	this study		this study		this study		Baird and Moe (1978)		Amaral (1977)		Manuwal and Boersma (1978)		Hatch et al. (1979)	

[a]Theragra chalcogramma and Eleginus gracilis combined.

Table 32. Number and percent of individual prey items of different species delivered to Horned Puffin nestlings.

	Buldir Island 1975		Shumagin Islands 1976		Barren Islands 1976		Barren Islands 1977	
	No.	%	No.	%	No.	%	No.	%
Mallotus villosus-Capelin			34	21.1	14	73.7	26	44.8
Gadus macrocephalus-Pacific Cod			17	10.6			1	1.7
Trichodon trichodon-(Pacific) Sandfish			1	0.6	1	5.2	1	1.7
Ammodytes hexapterus-Pacific Sand Lance	22	42.3	107	66.5	3	15.8	30	51.7
Pleurogrammus monopterygius-Atka Mackeral	22	42.3						
Hexagrammos stelleri-Whitespotted Greenling					1	5.2		
Hemilepidotus jordani	1	1.9						
Unidentified fish			2	1.2				
Cephalopoda	7	13.5						
Source	this study		Moe and Day (1979)		Amaral (1977)		Manuwal and Boersma (1978)	

lance comprised a significant portion of the nestlings diet, but Capelin was not represented. On Middleton Island, sand lance comprised 60.0% of the prey delivered, with octopus and squid accounting for almost all of the other prey. On Buldir Island, Tufted Puffins delivered almost equal numbers of sand lance and squid and slightly lesser numbers of the sculpin, (Hemilepidotus jordani), while Horned Puffins delivered equal numbers of sand lance and Atka Mackerel (Pleurogrammus monopoterygius), with almost all remaining prey items being squid.

On Chowiet Island, AK, in 1976, 12 loads of food delivered by Tufted Puffins consisted primarily of sand lance and Walleye Pollock and 20 loads delivered by Horned Puffins consisted chiefly of sand lance and Capelin (Lesciner and Burrell 1977). Observations in 1976 and 1977 of food carried by adult Horned Puffins on Ugaiushak Island, as well as partial bill loads found within the Horned Puffin colonies, indicated that sand lance was by far the most numerous prey species delivered to young each year. Also, it appeared that Horned Puffins carried relatively fewer Capelin and more Walleye Pollock and/or Saffron Cod (Eleginus gracilis) in 1977 than did Tufted Puffins.

The information available from Alaskan puffin colonies indicates that while sand lance and Capelin are the primary sources of food for nestlings of both Tufted and Horned puffins, the relative importance of subsidiary prey types appears to be different between the two puffins. Squid and octopus are the most important subsidiary prey taken by Tufted Puffins, followed by cod, sculpin, and greenling. In contrast, the most important subsidiary prey taken by Horned Puffins are usually fish, especially greenling and cod, and these are followed in importance by squid and sandfish.

The universal importance of sand lance and Capelin in the diet of puffin nestlings at the different colonies, suggests that these two fish species are generally abundant and available to the puffins. As growth rates and fledging success of chicks are highest when sand lance and Capelin comprise 85-90% of the nestling diet (see below), selection probably favors adults taking these prey over subsidiary prey when sand lance and/or Capelin are abundant and available to the birds. However, when one of these species is not abundant or available in a particular year, as suggested by its low occurrence in the nestling diet, Tufted Puffins apparently fill the void by taking greater numbers of the other of these two species (e.g., Ugaiushak Island 1976, Barren Islands 1976). If neither sand lance nor Capelin are abundant or available, then both Tufted and Horned puffins feed to a greater extent on different subsidiary species (e.g., Buldir Island, Middleton Island).

Thus, under "typical" circumstances, when sand lance and/or Capelin are abundant and available, competition between Tufted and Horned puffins is minimal. When one of these fish species is low in abundance or availabilty, the mechanics of ecological segregation begin to operate, but it is not until both of the primary prey species are low in abundance or availability that the two puffin species become ecologically segregated in terms of prey fed to nestlings.

In two non-Alaskan studies, sand lance was also the predominant prey species delivered to Tufted Puffin nestlings. The frequency of prey species per bill load on Triangle Island, B.C., was 68%-sand lance; 23%-rockfish, (Sebastes sp.); 10%- Pacific Saury, (Cololabis

saira); 3%-Ratfish, (Hydrolagus colliei); and 7%-squid, (Gonatus anonychus) (Vermeer et al. 1979). The relative importance of prey species delivered to Tufted Puffin chicks on the Olympic Peninsula, WA, was, in decreasing importance, sand lance (Ammodytes), anchovy (Engraulis), seabass (Sebastoides), smelt (Hypomesus) (Cody 1973). These observations, in conjunction with those from Alaskan colonies (above), underline the extreme importance of sand lance to the feeding ecology of Tufted Puffins throughout the range of these birds.

The relative importance of different prey species may vary during the nestling period in certain years and colonies; however, the patterns of variation are not consistent. Capelin were consistently fed to Tufted Puffin chicks on Sitkalidak Island throughout the nestling period. However, Capelin became less important in terms of weight and other species, such as Pacific Sandfish and Walleye Pollock, became more important as the summer progressed (Baird and Moe 1978). Baird and Moe also found that monospecific loads of Capelin decreased during the nestling period, while monospecific loads of sand lance increased, suggesting a possible increase in the availability of the latter species. Similarly, during a 2.5-week period in August, the relative number of sand lance delivered to Horned Puffin chicks on the Shumagin Islands increased markedly, while the number of Capelin decreased (Moe and Day 1979). This trend was the opposite for Tufted Puffins on Ugaiushak Island in 1977 and the almost total breeding failure of Tufted Puffins on Triangle Island, B.C., was attributed to the decrease in the availability of sand lance during the latter stages of the nestling period and the subsequent failure of the birds to switch to another food source (Vermeer et al. 1979).

The seasonal variation in the relative importance of different prey species, particulary sand lance and Capelin, in the diets of puffin nestlings presumably reflects changes in the abundance and availability of these prey. Both sand lance and Capelin undergo seasonal changes in depth distributions correlated with stages in their life cycle (Hart 1973, Harris and Hartt 1977). The variation in the composition of these two prey species in the diet of nestling puffins may reflect changes in their depth distribution as influenced by local variations in physical and biological oceanographic factors.

Size of Prey

Most fish fed to Tufted and Horned puffin nestlings ranged in length from 60-100 mm (Tables 33-34). There was no significant difference in the size of sand lance delivered to Tufted and Horned puffin chicks on Buldir Island, however, Tufted Puffins fed their chicks significantly longer Atka Mackeral and squid than did Horned Puffins.

Sand lance taken by Tufted Puffins on Ugaiushak Island were significantly larger in 1977 than in 1976 but were not significantly different in size from those fed to Tufted Puffin chicks on Buldir Island in 1976. Similarly, Capelin delivered to Tufted Puffin chicks in 1977 were significantly larger than in 1976.

In both years on Ugaiushak Island, the mean length of sand lance delivered to chicks tended to increase during the nestling period. This same pattern was also observed on Middleton Island for sand

Table 33. Length (mm) of individual prey items delivered to Tufted Puffin nestlings.

Species		Length (mm) Buldir Island 1975	Ugaiushak Island 1976	Ugaiushak Island 1977	Middleton Island 1978
Onchorynchus keta- Chum Salmon	N			2	
	$\bar{x}$			149.0	
	s			18.4	
	Max.			162	
	Min.			136	
O. gorbuscha- Pink Salmon	N				1
	$\bar{x}$				154
Mallotus villosus- Capelin	N		10	28	
	$\bar{x}$		59.6	97.1	
	s		13.8	19.0	
	Max.		78	136	
	Min.		40	82	
Theragra chalcogramma Walleye Pollock	N		13	15[a]	
	$\bar{x}$		63.3	74.3	
	s		26.7	8.5	
	Max.		147	89	
	Min.		43	64	
Eleginus gracilis- Saffron Cod	N		11	15[a]	
	$\bar{x}$		66.9	74.3	
	s		18.6	8.5	
	Max.		90	89	
	Min.		44	64	
Trichodon trichodon- Pacific Sand Fish	N				1
	$\bar{x}$				78.0
Lumpenus sp.	N		1		
	$\bar{x}$		54		
Zaprora silenus- Prowfish	N				2
	$\bar{x}$				106.5
	s				16.3
	Max.				118
	Min.				95
Ammodytes hexapterus- Pacific Sand Lance	N	12	346	124	54
	$\bar{x}$ age 0	78.8	63.0	79.0	87.5(n=42)

Table 33. Continued.

Species		Length (mm) Buldir Island 1975	Ugaiushak Island 1976	Ugaiushak Island 1977	Middleton Island 1978
Ammodytes hexapterus-age 1					131.2(n=10)
Pacific Sand Lance	age 2				161.0(n=2)
	s	32.9	9.8	9.2	
	Max.	178	127	117	
	Min.	36	46	60	74
Scorpaenidae	N		1		
	$\bar{x}$		35		
Pleurogrammus monopterygius-	N	3			
Atka mackeral	$\bar{x}$	99.7			
	s	28.0			
	Max.	132			
	Min.	82			
Hemilepidotus jordani	N	13			
	$\bar{x}$	30.5			
	s	1.2			
	Max.	33.0			
	Min.	29.5			
Aspidophoroides bartoni	N	1			
	$\bar{x}$	41.5			
Cephalopoda	N	10			8
	$\bar{x}$	107.7			56.6
	s	23.0			
	Max.	149.0			72
	Min.	84			31
Octopoda	N			1	14
	$\bar{x}$				71.9
	s				
	Max.				90
	Min.				51
Source		this study	this study	this study	Hatch et al. (1979)

[a]Theragra chalcogramma and Eleginus gracilis combined

Table 34. Length (mm) of individual prey items delivered to Horned Puffin nestlings on Buldir Island, 1975.

Species		Length (mm)
Ammodytes hexapterus- Pacific Sand Lance	N	18
	$\bar{x}$	81.1
	s	22.72
	Max.	164.0
	Min.	56.0
Hemilepidotus jordani	N	1
	$\bar{x}$	30.0
Pleurogrammus monopterygius Atka Mackeral	N	20
	$\bar{x}$	84.2
	s	8.68
	Max.	115.0
	Min.	68.5
Cephalopoda	N	7
	$\bar{x}$	65.9
	s	21.20
	Max.	93.5
	Min.	30.0

lance (Hatch et al. 1979), on Sitkalidak Island, AK, for sand lance and Capelin (Baird and Moe 1978), and on the Olympic Peninsula, WA, for apparently all prey (Cody 1973). As most sand lance fed to puffin nestlings were juveniles (see Blackburn 1979), the progressive increase in size during the nestling period probably reflects the growth of sand lance during this period (Blackburn 1979) and not selection of progressively larger prey by the birds.

Growth Rates of Nestlings

Growth rates were obtained from 64 single chicks amd 15 sets of twins raised under different conditions (Table 27). Although 28 sets of twins were originally studied, one chick in each of 13 sets was either rejected by the attending adults and was driven from the nest-site or was forcibly kept by its nest-mate from food delivered by the adults, causing it to die of starvation. Similar results for twinning experiments have been reported for Rhinoceros Auklets (Summers and Drent 1979) and Common Puffins (Nettleship 1972, Corkhill 1973, Harris 1978). I submit that this "twinning effect," i.e., the effects of adult rejection and of sibling aggression, was the primary cause for failure of both members of the 13 sets in this study to survive (Table 27), and that death was not related to the amount of food delivered by the adults.

Based on growth rates (Figure 4, Table 35), it appeared that unfed single Tufted Puffin chicks received progressively greater amounts of food and/or food of greater nutritional value each year

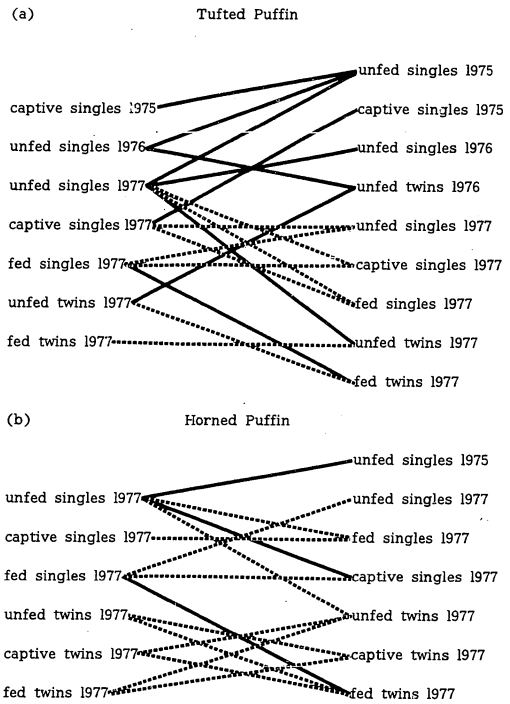


Figure 4. Relative growth rates of Tufted (a) and Horned (b) puffin chicks raised under different conditions. Chicks in situations at left grew significantly faster than (solid line) or at same rate as (dashed line) chicks in situations at right.

Table 35. Slopes of regression lines for growth of Tufted and Horned puffin chicks reared under different conditions.

Year	Situation	Tufted Puffin		Horned Puffin	
		Slope	s	Slope	s
1975	Unfed singles	3.33	0.524	4.45	0.374
	Captive singles	10.48	0.859		
1976	Unfed singles	15.89	0.415		
	Unfed twins	7.02	0.995		
1977	Unfed singles	18.38	0.614	11.52	0.831
	Captive singles	17.82	0.559	7.34	1.911
	Fed singles	17.82	1.007	12.84	1.389
	Unfed twins	14.43	1.122	10.09	1.334
	Captive twins			9.51	0.399
	Fed twins	14.77	0.803	6.64	2.028

from 1975 to 1977, the difference being much greater between 1975 and 1976 than between 1976 and 1977. Unfed, captive, and fed singles in 1977 all grew at the same rate, suggesting that adults in 1977 were feeding chicks close to the maximum amount of food they could utilize. The captive chick in 1975 grew significantly faster than unfed singles that year but did grow as fast as captive chicks raised in 1977, as might be expected. This may have been because the partially digested fish and canned fish fed in 1975 was of lower nutritional value than the fresh whole fish fed in 1977.

Although unfed singles in 1976 grew significantly faster than unfed singles in 1975, unfed twins in 1976 grew significantly slower than unfed singles that year. The fate of unfed twins in 1976 indicates that the quantity and/or quality of food available to chicks that year, although apparently greater than in 1975, was insufficient for both chicks to fledge successfully. At the time I left the island, neither of the twins had fledged; both were 44 days old, and their weights were 189 and 380 g. The heavier of the two chicks weighed an average of 207 g less than six unfed single chicks of the same age. In 1977, I examined their burrow and found the remains and aluminum band of the lighter chick. Whether the heavier of the two chicks successfully fledged the previous year is not known.

In 1977, unfed and fed singles grew significantly faster than unfed and fed twins, respectively, which grew at the same rate; but, unfed twins in 1977 grew significantly faster than unfed twins in 1976, again suggesting that the quantity and/or quality of food was greater in 1977 than 1976. The lack of a significant difference in 1977 in the

growth rates of unfed and fed twins and their slower growth rates as compared to singles in 1977 may have been the result of two factors: 1) the 100 g of additional food was insufficient to promote a difference, and/or 2) the twins expended more energy interacting between themelves than would be expended by a single chick.

As with Tufted Puffins, the significantly faster growth rates of unfed, captive, and fed Horned Puffin singles in 1977 than for unfed singles in 1975 suggests that the quantity and/or quality of food was greater in 1977 than 1975. Further, the lack of a significant difference in growth rates of unfed and fed singles in 1977 indicates that adults were probably delivering close to the maximum amount of food the chicks could utilize. The slightly slower rate of growth of captive than unfed and fed singles in 1977 was likely the result of chicks being taken into captivity before brooding had been terminated by the adults.

There was no significant difference in the growth rates of unfed, captive, and fed Horned Puffin twins; however, unlike Tufted Puffins, unfed Horned Puffin twins grew at the same rate as unfed singles, i.e., near the maximum rate of growth. That fed Horned Puffin twins grew significantly slower than fed singles was probably the result of the pair of fed twins having to divert more energy into body heat. These chicks were raised in an exposed nest-site and were subject to the chilling effect of almost continuous rain during the 20 days of the experiment.

Results from these experiments indicate: 1) probably neither Tufted nor Horned puffins were able to successfully raise to fledging

single chicks in 1975, 2) Tufted Puffins were able to raise single chicks but not twins in 1976, and 3) both Tufted and Horned puffins were able to raise both single chicks and twins in 1977. The most likely explanation for these results is that the quantity and/or quality of food available to chicks increased progressively during each of these three years. This assumption is lent further credibility by an analysis of growth rates of unfed single Tufted and Horned puffin chicks raised at a variety of colonies during these years (Table 36). Growth rates of Tufted Puffin chicks at four colonies in 1976 were all greater than for chicks on Buldir Island in 1975 and growth rates of chicks at three colonies in 1977 were all greater than for those in 1976. Similarly, growth rates of Horned Puffin chicks at three colonies in 1976 were all greater than for chicks on Buldir Island in 1975; however, the differences in growth rates between Horned Puffin chicks raised in 1976 and 1977 were less marked than for Tufted Puffin chicks in those years.

Conclusions

Much of the variation in the breeding success of Tufted and Horned puffins between colony-years may be explained in terms of the food and feeding ecology of nestlings. In the absence of human disturbance, fledging success is probably the most variable component of breeding success between colony-years. Although predation and weather-related factors may affect fledging success in certain colony-years, the most important influence on the fledging success of puffins

Table 36. Slopes of regression lines for growth of Tufted and Horned puffin chicks reared under different colony-years.

Year	Colony	Tufted Puffin		Horned Puffin	
		Slope	s	Slope	s
1975	Buldir Island	3.33	0.524	4.45	0.374
1976	Chowiet Island	8.55	0.565	6.937	0.628
	Wooded Islands	14.97	0.435		
	Ugaiushak Island	15.89	0.415		
	Shumagin Islands	16.12	0.672	13.36	0.712
	Barren Islands	16.14	0.788	8.92	0.705
1977	Barren Islands	16.95	0.763	8.88	1.099
	Sitkalidak Island	17.12	0.615		
	Ugaiushak Island	18.95	0.614	11.52	0.831

appears to be the quantity and/or quality of food available to the nestlings. The relationship between fledging success and variations in the quantity and/or quality of nestling food between colony-years may be assessed in terms of four parameters: length of the nestling period, weight of bill loads carried to young, the dominant prey species comprising bill loads, and the growth rate of nestlings (Tables 37-38).

The minimum length of the nestling period for both Tufted and Horned puffins reflects a characteristic and inherent growth pattern which presumably has been optimized through natural selection (Ricklefs 1967, Sealy 1972). However, within this inherent growth pattern there is a general negative correlation between the length of nestling period and growth rate, i.e., the slower a chick grows, the longer it remains in the nest. Growth rates of Tufted and Horned puffins, in turn, are related to the weight of bill loads delivered and to the composition of bill loads. In general, growth rates tend to be highest when 1) the weight of bill loads are the heaviest, indicating that the more food a chick receives the faster it grows; 2) sand lance and/or Capelin comprise at least 85-90% of the prey items fed to nestlings; and 3) sand lance and Capelin are the dominant prey species than when either one of these species comprise virtually all of the prey fed to the young. When sand lance and/or Capelin comprise less than 85-90% of the total prey items, growth rates tend to be highest when other species of fish are fed to young than when squid are fed to the nestlings. Further, when squid are among the dominant prey fed to young, the weight of bill loads is greater than when other fish species are fed; however, growth rates of chicks are lower, suggesting that squid may be of less nutritional value than fish for puffin nestlings.

Table 37. Summary of data for selected aspects of the breeding biology and feeding ecology related to fledging success of Tufted Puffins in different colony-years.

	Buldir Island 1975	Ugaiushak Island 1976	Barren Islands 1976	Chowiet Island 1976	Ugaiushak Island 1977
Length of the Nestling Period (days)	36-46	44.8	47	50.4	41.8
Weight per Bill Load (g)	11.9	9.7	14.9	7.5	14.4
Dominant Prey Species[a]	sand lance (36.5)	sand lance (88.8)	Capelin (94.5)	sand lance/ Walleye Pollock	sand lance (82.0)
	squid (33.3)	gadids (6.3)	squid (3.6)		Capelin (13.0)
	Hemilepidotus jordani (20.6)	Capelin (2.6)	Prowfish (1.8)		gadids (4.9)
Growth Rate[b]	3.33	15.90	16.14	8.55	18.37
Fledging Success	probably 0%	80-86%	69%	56%	62-95%
Source	this study	this study	Amaral (1977) Burrell (1977)	Leschner and	this study

Table 37. Continued

	Barren Islands 1977	Triangle Islands 1977	Sitkalidik Island 1977
Length of the Nestling Period (days)		47	35-49
Weight per Bill Load (g)	20.4	9.7-18.7	19.3
Dominant Prey Species[a]	Capelin (57.0)	sand lance	Capelin (64.9)
	sand lance (30.3)	rockfish	sand lance (25.8)
	gadids (6.3)	Pacific Saury	gadids (3.7)
Growth Rate[b]	16.95		17.12
Fledging Success	79%	1.9%	88%
Source	Manuwal and Boersma (1978)	Vermeer et al. (1979)	Baird and Moe (1978)

[a]number in parentheses indicates percent by number of all individual prey items carried to young

[b]figures represent slopes of regression line from day 5 to day 25

Table 38. Summary of data for selected aspects of the breeding biology and feeding ecology as related to fledging success of Horned Puffins in different colony-years.

	Buldir Island 1975	Barren Islands 1976	Chowiet Island 1976	Shumagin Islands 1976	Ugaiushak Island 1977	Barren Islands 1977
Length of the Nestling Period (days)	41-43	40	39		34	
Weight per Bill Load (g)	11.0	10.7	7.9	13.8		17.0
Dominant Prey Species[a]	Sand lance (42.3)	Capelin (73.7)	Sand lance	Sand lance (66.5)	Sand lance	Sand lance (51.7)
	Atka Mackeral (42.3)	Sand lance (15.8)	Capelin	Capelin (21.1)	Capelin	Capelin (44.8)
	Squid (13.5)	Sandfish (5.2)		Pacific Cod (10.6)		Pacific Cod (1.7)
		Greenling (5.2)				Sandfish (1.7)
Growth Rate[b]	4.45	8.93	6.94	13.36	11.52	8.88
Fledging Success	probably 0%	36%	49.5%	72%	9-91%	69%
Source	this study	Amaral (1977)	Leschner and Burrell (1977)	Moe and Day (1979)	this study	Manuwal and Boersma (1978)

[a]number in parentheses indicates percent by number of all individual prey items carried to young.

[b]figures represent slope of regression line from day 5 to day 25.

Thus, for those colony-years considered, the most important factor influencing fledging success of Tufted and Horned puffins appears to have been the presence of sand lance and Capelin in the diet of nestlings. The low growth rates and fledging success of both Tufted and Horned puffins in 1975 were associated with the relatively low proportions of sand lance and the absence of Capelin in the nestlings' diet. In 1976, sand lance or Capelin comprised rather high proportions of prey items fed to Tufted Puffin nestlings and both growth rates and fledging success were higher than in 1975. The low occurrence or absence of one or the other of these major two prey items in 1976 were associated with lower growth rates and fledging success for Tufted Puffins than in 1977, when both sand lance and Capelin together comprised nearly 90% of all food items fed to young. An exception to this was Triangle Island, where no Capelin were taken and where the number of sand lance taken decreased during the nestling period (Vermeer et al. 1979).

Although fledging success was generally higher for Horned Puffins in 1977 than in 1976, the fact that growth rates were approximately the same both years indicates that the observed differences in fledging success were probably not related to food availability. In both years, sand lance and Capelin comprised the majority of all prey fed to nestlings. Why Horned Puffins were able to take both sand lance and Capelin in 1976, when Tufted Puffins took primarily sand lance or Capelin remains unclear. Possibly, both prey species were present closer to shore, where Horned Puffins foraged, than farther offshore, where one or the other prey species was more abundant and

where Tufted Puffins concentrated their foraging. The more equal representation of both sand lance and Capelin in the diets of Tufted and Horned puffins in 1977 than in 1976, suggest that both prey species were generally more available in 1977.

SUMMARY AND CONCLUSIONS--CHAPTER I

Tufted and Horned puffins differ in their preference of nesting habitats. Generally, Tufted Puffins nest in earthen burrows along cliff-edges or on steep seaslopes and less frequently in rock crevices. Horned Puffins, on the other hand, typically nest in rock crevices primarily in talus slopes but also under beach boulders and cliff-faces.

The arrival at the breeding colonies of Tufted Puffins occurs 2 to 3 mo and Horned Puffins 1 to 2 mo later at the northern and southern limits of their ranges. At the same colony, each species generally arrives within the same 1- to 2-week period each year. Once at the colony, Tufted and Horned puffins show marked differences in their patterns of colony settlement. The interval between arrival and land-coming is usually 1 to 2 weeks for Tufted Puffins and less than 1 week for Horned Puffins. Whereas land-coming generally coincides with continuous occupancy for Horned Puffins, the interval between these two events is typically several weeks for Tufted Puffins. During this time, Tufted Puffins exhibit a quasi-cyclic pattern of attendance at the breeding colony, being present for several days and then absent (at sea) for an equal period of time. Such cyclic attendance patterns may be related to this species' habit of feeding offshore, whereas Horned

Puffins feed inshore. Cyclic attendance patterns of Tufted Puffins are usually abated and continuous occupancy established within a week of, and sometimes coinciding with, the onset of egg-laying. Egg-laying in Horned Puffins generally follows the establishment of continuous occupancy by 2 to 3 weeks. The total length of the pre-egg stage increases in length at higher latitudes for Tufted Puffins but remains relatively stable for Horned Puffins.

Horned Puffins appear to be more social than Tufted Puffins both on land and on water, where they form tighter rafts and associate more in pairs. Both species share a number of behaviors in common (courtship ceremony, billing, fly-bys, bill-gaping, fighting, wing-flapping, preening, and head-dipping), but each species also has certain behaviors either unique to itself or performed more frequently or in different contexts than by the other species (head-jerking, bowed-head display, landing display). Although Tufted Puffins generally defend a territory including the burrow entrance, approach path, and landing/loafing sites, Horned Puffins probably defend only the nest itself.

Tufted and Horned puffins each have four basic vocalizations: a single note, call, a purring call, a bi-syllabic call, and a multi-note call--each showing differing degrees of interspecific variability.

Because burrows are more vulnerable than rock crevices to destructive natural forces, Tufted Puffins spend more time each year preparing nest-sites for egg deposition than Horned Puffins. Old burrows may be re-excavated each year prior to egg-laying, however, new burrows are not dug in the same year in which they are used for

breeding. Tufted and Horned puffins generally construct their nests only several days before egg-laying. Nests of both species typically consist of grasses, umbels, and feathers. The size of the nest is usually positively correlated with the amount of vegetation in the immediate vicinity of the nest-site.

Experiments with Tufted Puffins on Buldir Island indicated that at least 29% of the birds studies exhibited nest-site tenacity; however, the true value in the absence of human disturbance was probably much higher. Nest-site tenacity was strongly suspected in Horned Puffins, based on the repeated use of particular nest-sites in successive years.

In most cases, nesting habitats of Tufted and Horned puffins are used by at least one and sometimes as many as nine other seabird species. Thus, in some colonies, the potential for interspecific competition for nest-sites may be great. Also, in some colonies, Tufted Puffins cohabit burrows with one of several nocturnal seabird species. Presumably, the sharing of a nest-site between a diurnal and a nocturnal species reduces potential competition.

At the same latitude, peak egg-laying is generally 1-3 weeks earlier for Tufted than Horned puffins and occurs approximately 1 mo and 2 weeks earlier, respectively, at their southern than northern breeding limits. Peak egg-laying generally occurs between late May and mid-June for Tufted Puffins and between mid-June and early July for Horned Puffins. Dates of egg-laying for Tufted Puffins appear to be more influenced by adverse nest-site conditions (e.g., the presence of ice, mud, or water) than for Horned Puffins.

Tufted and Horned puffin eggs are ovate in shape with a tendency toward ovate-pyriform. Eggs of both species are a dull creamy-white or pale bluish-white with various amounts of spots and/or scrawls of gray, blue, green, reddish-brown, and brown. Tufted Puffin eggs are significantly longer, wider, and heavier than Horned Puffin eggs, but the proportionate egg weight of Horned Puffins is significantly greater than that of Tufted Puffins. The mean egg weight loss during incubation is approximately the same for both species, averaging 12-13%.

At some time in their evolutionary past, Tufted and Horned puffins laid a two-egg clutch rather than the single-egg clutch laid today. Both species, however, still retain two brood patches. Experiments conducted to see if Tufted Puffins would incubate two eggs revealed that concomitant with the selective forces favoring the laying of one egg rather than two, Tufted Puffins lost the "drive" to incubate two eggs in favor of one.

Both Tufted and Horned puffins may lay a replacement egg if the first egg is lost. Seventy percent of the Tufted Puffins and 30% of the Horned Puffins studied on Ugaiushak Island layed replacement clutches 10-21 and 16-20 days, respectively, after the first egg was removed. In both species, the weight and volume of the first eggs were significantly greater than those of replacement eggs. None of the Tufted Puffins and possibly one of the Horned Puffins laid a second replacement egg. Defeathering of brood patches in Tufted and Horned puffins began several days immediately preceding egg-laying. Refeathering began during the late incubation period and continued

throughout the nestling period. Tufted Puffin brood patches were slightly larger than those of Horned Puffins, presumably reflecting their larger eggs.

Both male and female Tufted and Horned puffins participate in incubation. Sexes generally exchange duties at least once daily, although a 4-5 day incubation rhythm was suspected on Buldir Island in 1975. Birds of both species frequently leave their eggs unattended for several hours each day and sometimes for a day or longer.

There is considerable intraspecific variation in the length of incubation for Tufted and Horned puffins. The mean length of incubation for Tufted Puffins (45.4 days) is approximately five days longer than for Horned Puffins (40.8 days).

Tufted and Horned puffin chicks hatch with the aid of a single egg tooth located on the tip of the upper mandible. In both species, the egg tooth usually disappears gradually several weeks after hatching, although it sometimes drops off abruptly.

After hatching, Tufted Puffins brood their chicks more or less continuously for 1-3 days while Horned Puffins brood continuously for 5-7 days. The shorter brooding period in Tufted than Horned puffins has probably related to the former's feeding further offshore.

Tufted Puffin chicks occur in two color phases, white and gray, in both the downy and juvenal plumages. Data for two colonies showed that 6.2% and 2.5% of chicks had white belly down in downy plumage and 23.5% and 25% of chicks had white belly contours in juvenal plumage.

There is considerable intraspecific variation in the length of the nestling period for Tufted and Horned puffins. Reported nestling period lengths for Tufted Puffins ranged from 41 to 59 days and for Horned Puffins from 36 to at least 43 days. This variability is attributed to the concert of factors related to the food and feeding of young.

Fledging of Tufted and Horned puffins occurs primarily at night. Fledglings of both species are apparently unable to fly at the time of their departure and, thus, flutter to the sea from cliff-tops and sea-slopes. Once on the water, fledglings swim immediately out to sea and are independent of their parents.

In all colony-years studied, laying success of Tufted Puffins ranged from 47% to 76% with an average of 50-60%. Hatching success ranged from 43% to 100%, with an average of roughly 55-60%. This average value in hatching success is probably low as a result of human disturbance and a natural hatching success rate of 75-90% is suggested. Other than human disturbance, egg mortality of Tufted Puffins was attributed to predation, flooding of nest-sites, and death of the embryo at hatching. Tufted Puffins probably have a natural desertion rate of their eggs of 5-15%.

Hatching success of Horned Puffins ranged from 56% to 100% with an average of roughly 80% for all colony-years. Eggs of Horned Puffins were generally less subject to predation and flooding than those of Tufted Puffins; most egg mortality being the death of the embryo at hatching.

Fledging success of Tufted and Horned puffins was extremely variable between colony-years, but averaged 60-70% for Tufted Puffins

and 53-77% for Horned Puffins. In both species, most chick mortality occurred within two weeks after hatching. In the absence of terrestrial predators, the most likely cause of death in older chicks was starvation.

Tufted Puffin males showed a significant decrease in body weight of 8.5% between the pre-egg and early nestling stages and a significant increase in weight of 2.5% between the early and late nestling stages. Body weight of females followed the same general pattern as males, but differences between breeding stages were not statistically significant probably due to small sample sizes. The pattern of weight loss followed by weight gain was also illustrated by the index of fat content at various stages. Horned Puffin body weights showed no significant fluctuation during the breeding season; however, fat content decreased continuously throughout the breeding season in both males and females.

Subadult Tufted and Horned puffins arrived at the breeding colonies in July, roughly 2.5 mo after the arrival of adults. Subadult birds were most frequent in areas of the colonies not used by adults. Although both sexes were present, subadults showed no evidence of pairing. The arrival of subadult Tufted Puffins coincided with a dramatic increase in burrow excavation and reconstruction.

Avian predators of adult Tufted and Horned puffins include Bald Eagles, Snowy Owls, and Peregrine Falcons. The impact of these predators on any single puffin population is probably minimal. The major mammalian predators of adult Tufted and Horned puffins are Arctic and Red foxes and River Otters. Generally, the influence of

these predators is not so much direct predation but a restriction of the puffins to more protected nest-sites. Both Glaucous-winged Gulls and Parasitic Jaegers are cleptoparasites of Tufted and Horned puffins, but their cleptoparasitism does not have a significant impact on the success rate of puffins feeding chicks.

Tufted and Horned puffins capture their prey by pursuit diving, feeding singly and in monospecific and mixed species assemblages. The foraging habitat used by Tufted Puffins varies considerably within a single breeding season at the same colony and among colonies. Sometimes Tufted Puffins feed in offshore or oceanic waters until the beginning of the nestling period after which they forage primarily in inshore waters; other times they forage in inshore, offshore, or oceanic waters throughout the breeding season. On the other hand, Horned Puffins at most colonies tend to forage in inshore waters throughout the breeding season. The apparent versatility in foraging habitats used by Tufted Puffins may be an adaptation to reduce interspecific competition with Horned Puffins at times when food is limiting.

Almost all prey remains found in puffin stomachs (fish vertebrae, squid beaks, polychaete paragnaths, shell fragments, and plastic) were either not digestible or were being digested at a slow rate. Based on the relative frequency of these prey remains, fish were the predominant prey eaten by adult Tufted and Horned puffins, although in some colony-years squid were eaten in equal or greater numbers. Because of the difference in the digestion rate of different prey, the importance of fish and squid in the diets of Tufted and Horned puffins is probably over-estimated while the importance of soft-bodied organisms without "hardparts" is under-estimated.

Relatively more immature Tufted and Horned puffins on Buldir Island ingested fish and polychaetes than did adults. The incidence of ingested squid between age classes was similar in Tufted Puffins but slightly lower in immature than adult Horned Puffins.

The predominance of different food types in the stomachs of Tufted and Horned puffins varied with different stages of the breeding period on Buldir Island. Polychaetes were only evident during the pre-egg stage for Tufted Puffins and only during the incubation and hatching stages for Horned Puffins. Fish were highest during the nestling stage for both species. The frequency of squid remained high throughout all breeding stages for Tufted Puffins but decreased with time for Horned Puffins.

Over one-quarter of the 228 Tufted and Horned puffins collected on Buldir and Ugaiushak islands contained plastic in their stomachs. Plastic was more common in puffins collected on Buldir Island than on Ugaiushak Island. On Buldir Island, the frequency of plastic in adult Horned Puffins was over three times greater than in adult Tufted Puffins, but plastic was present in roughly twice as many immature Tufted as Horned puffins.

Throughout Alaska, Tufted and Horned puffins exhibit seasonal, yearly, and geographic variation in their diets. Although fish is the major prey item taken by both species, Horned Puffins appear to take a greater variety of fish, especially inshore, subtidal species, than do Tufted Puffins, which more regularly supplement their diet with squid. Despite these general preferences, both species appear to be flexible in their dieting preferences and are opportunistic in taking advantage of locally or temporarily abundant prey types.

Tufted and Horned puffins carry food in their bills back to their nestlings. Bill loads of food are dropped on the floor of the nest-sites where they are retrieved by the chicks. Both sexes share in the feeding of young.

Food generally is delivered in the early to mid-morning and in late afternoon to early evening during the early nestling period and in the early to mid-morning, mid-afternoon, and just prior to nightfall in the late nestling period. Although there is considerable variation in the rate at which puffins feed their chicks, older chicks generally receive more bill loads of food each day than younger chicks.

The number of prey delivered per load varied considerably between colony-years, with a range in means of 3.4 to 10.1 for Tufted Puffins and 1.5 to 12.6 for Horned Puffins. The size of loads did not vary consistently during the nestling period. In general, both Tufted and Horned puffins delivered 10-20 g of food per bill load, but, there was considerable variation among colony-years and within the nestling period at the same colony.

Data from Alaskan puffin colonies indicate that sand lance and Capelin are the primary sources of food for nestlings of both Tufted and Horned puffins. The relative importance of subsidiary prey types is different between the two puffin species. In Tufted Puffins, squid and octopus are the most important subsidiary prey, followed by cod, sculpin, and greenling. In Horned Puffins, the most important subsidiary prey are fish, especially greenling and cod, followed by squid and sandfish. When either sand lance or Capelin is not abundant or available in a particular year, Tufted Puffins take greater numbers of

the other of these two species. If neither of these species are abundant or available, both Tufted and Horned puffins feed to a greater extent on subsidiary prey. Thus, when sand lance and/or Capelin are abundant and available, there is little competition between Tufted and Horned puffins. However, when one of the fish species is low in abundance or availability, the mechanics of ecological segregation begin to operate. It is not until both of the primary prey species are low in abundance or availability that Tufted and Horned puffins become ecologically segregated in terms of prey fed to nestlings.

The relative importance of different prey species in the diets of Tufted and Horned puffin nestlings may vary during the nestling period, but the pattern of variation is not consistent between colony years.

Most fish fed to Tufted and Horned puffin nestlings range in length from 60 to 100 mm. Generally, the size of prey increases gradually during the nestling period, presumably reflecting growth of individual prey.

Growth rates of Tufted and Horned puffin chicks under natural and experimental conditions on Buldir Island in 1975 and Ugaiushak Island in 1976 and 1977 revealed that feeding conditions were least favorable in 1975 and were progressively more favorable in 1976 and 1977. While it is doubtful that either Tufted or Horned puffins provided sufficient food to fledge single chicks in 1975, Tufted Puffins were able to fledge single chicks but not twins in 1976. Tufted and Horned puffins were able to fledge both single chicks and probably twins in 1977. Growth rates of Tufted and Horned puffins at other

Alaskan colonies also reflected more favorable feeding conditions in 1977 than 1976.

Fledging success of Tufted and Horned puffins was highest in those colony-years when sand lance and Capelin comprised at least 85-90% of the prey items fed to nestlings. In general, this high composition of sand lance and Capelin was positively correlated with heavier bill loads, faster growth rates, and shorter nestling periods.

CHAPTER II: COMPARATIVE BIOLOGY OF THE PUFFINS: LUNDA CIRRHATA, FRATERCULA CORNICULATA, F. ARCTICA, AND CERORHINCA MONOCERATA

This chapter is a monograph of the world's four species of puffins. Information presented in Chapter I on Tufted and Horned puffins is compared with that largely available in the literature for Rhinoceros Auklets and Common Puffins to provide a synthesis of information on the natural history of this alcid tribe.

SYSTEMATIC RELATIONSHIPS

The alcids (Family Alcidae) apparently diverged from an ancestral charadriiform stock (Kaftanowski 1951, Stettenheim 1959, Hudson et al. 1969) in the early Paleocene (Storer 1960) . Differentiation within the family began in the Pacific Basin as early as the late Eocene and was probably complete by the mid-Miocene (Storer 1960, Udvardy 1963, Brodkorb 1967). The family Alcidae is generally divided into seven tribes (Storer 1945, 1960): 1) the auks and murres (Alca, Pinguinus [now extinct], Uria), 2) the guillemots (Cepphus), 3) Marbled and Kittlitz's murrelets (Brachyramphus), 4) the other murrelets Endomychura, Synthliboramphus), 5) the Dovekie (Plautus), 6) the auklets, (Ptychoramphus, Aethia, Cyclorrhynchus), and 7) the puffins (Cerorhinca, Fratercula, Lunda).

Dispersal from the center of differentiation in the North Pacific to the Atlantic probably occurred through the North American arctic at times when the Bering Strait was open (Udvardy 1963). Today, 16 species breed only in the Pacific, 3 only in the Atlantic, and 3 breed in both the Pacific and Atlantic.

Puffins are apparently most closely related to the auklets, with Cerorhinca in many ways intermediate between the puffins and the auklets (Storer 1945). The earliest fossil remains of any of the three puffin genera are of Cerorhinca in the Middle Miocene (Brodkorb 1967), and the other two present-day genera, Lunda and Fratercula, probably evolved from early Cerorhince-like stock. The forerunner of the latter two genera had apparently come into existence by the late Pliocene. A possible forerunner of Lunda, the extinct genus Pliolund, has been reported from the San Diegan formation, San Diego, CA, of the Upper Middle Pliocene (Miller 1937).

According to Johansen (1958) and Udvardy (1963), "Protofratercula" migrated from the North Pacific to the North Atlantic in the late Pliocene where it evolved into a boreal form, Fratercula. Then, during the first interglacial of the Pleistocene, Fratercula spread back through the North American arctic to an area south of the Bering Strait. These populations became sufficiently isolated to form F. arctica in the Atlantic and F. corniculata in the Pacific. During subsequent Pleistocene glaciations, the range of arctica split into a high arctic and boreal refuge, and subspeciation occurred. Three subspecies of Fratercula arctica are generally recognized, based solely on differences in body size: the nominate subspecies F. a. arctica (Linnaeus), a

smaller southern subspecies, F. a. grabae (Brehm), and a larger northern subspecies, F. a. naumanni Norton. Belopol'skii (1957), however, recognized only F. a. naumanni and F. a. arctica, including F. a. grabae in the latter taxon. Pethon (1967) indicated that F. arctica is a species occurring on two clines, one running northeast and one northwest from the British Isles, and that it should be designated Fratercula arctica cl grabae/naumanni (L.), with a type locality of north Norway.

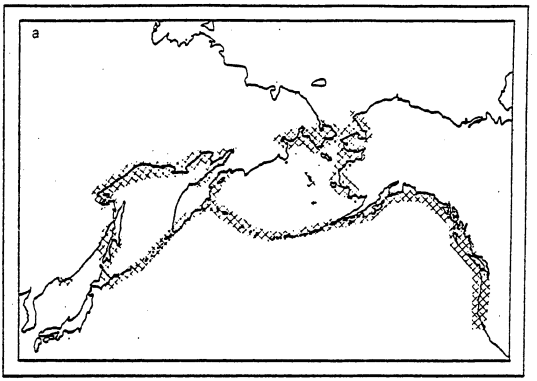
The three Pacific puffins differed in their ranges during the last glaciation and probably also during previous ones (Udvardy 1963). Cerorhinca monocerata apparently survived these glacial periods in refuges on both sides of the Pacific, but was absent from the intermediate area of the Aleutian arc. This species still exists today as two disjunct populations on either side of the Pacific, and there is no evidence that subspeciation has occurred. Udvardy (1963) reasoned that the unoccupied intermediate area was either not ecologically suitable for the establishment of the species or that the species has lost its colonizing ability by evolving a high degree of philopatry. Fratercula corniculata apparently survived as discontinuous relict populations in the Sea of Okhotsk, the central and eastern Aleutians, and the islands of the Bering Sea (or, if these were part of the land bridge, then coasts of the same) (Udvardy 1963). Lunda cirrhata apparently survived the glaciations along the Pacific coast of North America and in the central area of the Aleutian arc (Udvardy 1963). As with Cerorhinca monocerata, subspeciation in these latter two species has not been reported. Thus, four species of puffins exist today: Tufted

Puffin (Lunda cirrhata), Horned Puffin (Fratercula corniculata), Common Puffin (F. arctica), and Rhinoceros Auklet (Cerorhinca monocerata), with only the Common Puffin showing subspecific variability.

DISTRIBUTION AND ABUNDANCE

Breeding Distribution

The present-day breeding distribution of Tufted Puffins is shown in Figure 5a. In North America, Tufted Puffins breed from Cape Lisburne on Alaska's northwest coast, south along virtually the entire coastline of Alaska, including the islands of the Bering Sea, the Aleutian Islands, and the islands of the Gulf of Alaska and southeastern Alaska (Sowls et al. 1978). Far fewer numbers breed along the coasts of British Columbia, Washington, and Oregon and as far south as the Farallon Islands, CA, (AOU Checklist 1957, Drent and Guiguet 1961, Bartonek and Sowl 1972, Ainley and Whitt 1973, Frazer et al. 1973). The southern limit to their breeding range on the west coast of North America has retreated northward since the early part of this century, and their numbers at this southern extreme have declined markedly (Wheelock 1903, Howell 1917, Small 1960, Ainley and Lewis 1974). The rapid decline in Tufted Puffin numbers in southern California during the early 1900's has been attributed to oil pollution and the decline of the sardine (Sardinops caerulea) population in adjacent coastal waters (Ainley and Lewis 1974).



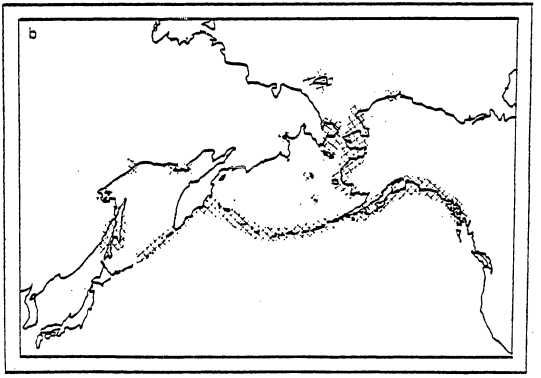
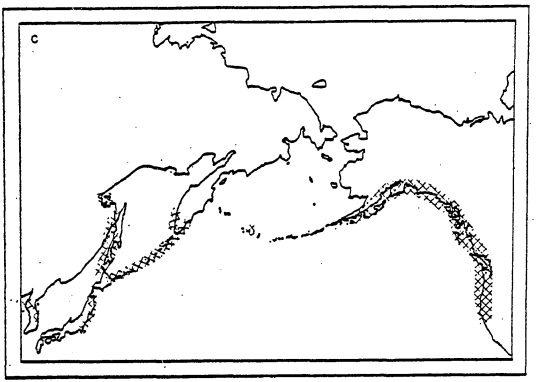


Figure 5. Breeding distribution of Tufted Puffins (a), Horned Puffins (b), Rhinoceros Auklets (c), and Common Puffins (d).



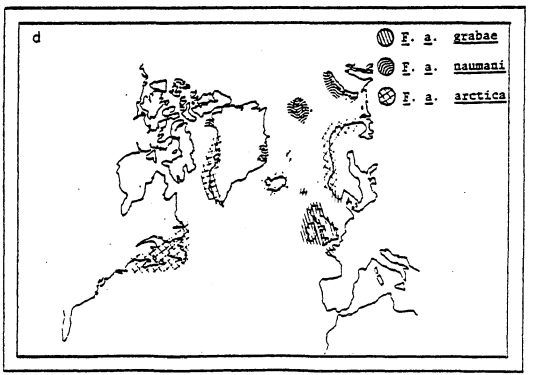


Figure 5. Continued

On the Asian side of the Pacific Ocean, Tufted Puffins nest from the north coast of the Chukotsk Peninsula (including Kolyuchin Island), south to Alyumka Island in the Anadyr Estuary and along the coasts of Olyutorskii Bay and the Sea of Okhotsk as far south as the Shantar Islands. Tufted Puffins breed on both coasts of the Kamchatka Peninsula, the Kurile and Commander islands, Sakhalin, the Maritime Province, and south to southern Hokkaido (Daikoku Island near Akkeshi), which is apparently the southernmost limit of their breeding range on the Asian Coast (Stejneger 1885, Dement'ev and Gladkov 1951, Austin and Kuroda 1953, Gizenko 1955, Kozlova 1957, Murie 1959, Johansen 1961).

Although Tufted and Horned puffins are sympatric throughout much of their breeding ranges, Horned Puffins occur in more northerly areas than Tufted Puffins (Fig. 5b). The northernmost substantiated breeding site known for Horned Puffins is Cape Lisburne, on Alaska's northwest coast, although G. J. Divoky (pers. comm.) reported a possible breeding record in 1975 of this species on Seahorse Island, near Barrow, AK, approximately 400 km north of Cape Lisburne. Horned Puffins breed south along Alaska's entire coastline and offshore islands to Forrester Island, near the border of British Columbia (Sowls et al. 1978). As with Tufted Puffins, the number of Horned Puffins breeding at the southern limit of their range appears to have declined during this century (Heath 1915, Willett 1915, Sowls et al. 1978).

On the Asian side of the Pacific, Horned Puffins breed from the northern coast of the Chukotsk Peninsula, including Wrangel Island and Kolyuchin Island, south along the eastern and southern coasts of

that peninsula. They breed on Alyumka Island in the Anadyr Estuary but not along the coast of Anadyr Bay. They are apparently scarce or absent south from Alyumka Island to the Kamchatka Peninsula where they breed along the eastern coast. In the Gulf of Shelekhova they breed on the Kronitskii Peninsula, probably as far south as Cape Lopatka. From there, southward along the Okhotsk coast, they are again absent until the Taigonos Peninsula near Ayan. Horned Puffins breed on the Shantar Islands, the northernmost parts of the Maritime Province, on Sakhalin, throughout the Commander Islands, and as far south as the northern and central Kurile Islands (Stejneger 1885, Dement'ev and Gladkov 1951, Austin and Kuroda 1953, Gizenko 1955, Kozlova 1957, Murie 1959, Johansen 1961).

Rhinoceros Auklets have the narrowest breeding distribution of the three Pacific puffins (Figure 5c). They probably breed on Buldir Island in the eastern Aleutians, (G. V. Byrd, pers. comm.) but they are apparently absent from there eastward to the south side of the Alaska Peninsula, where they breed in low numbers. Moderate numbers of Rhinoceros Auklets breed along Alaska's southern coast in the Gulf of Alaska, including Middleton Island (Sowls et al. 1978). The center of distribution extends from southeastern Alaska, along the coast of British Columbia, to northern Washington (Drent and Guiguet 1961, Sowls et al. 1978, Vermeer et al. 1979). Breeding populations of Rhinoceros Auklets have been confirmed as far south as Goat Island, OR, and at Castle Island and South Farallon Island, CA (Osborne 1971), Ainley and Lewis 1974). In recent years new colonies have been established at the southern edge of their range, and there is

some evidence that previously existing colonies in that area have increased in size (Scott et al. 1974).

The north-south oscillation of the southern boundary of the Rhinoceros Auklets' breeding range probably reflects changing environmental conditions (Scott et al. 1974) and changes in the abundance of prey species (Ainley and Lewis 1974). The disappearance of this species from the Farallone Islands coincides with egg gathering, the introduction of Old World Rabbits (Oryctolagus cuniculus) in the late 1800's, and the collection of actual specimens (Ainley and Lewis 1974).

Little recent information is available on the distribution of Rhinoceros Auklets on the Asian coast, but Dement'ev and Gladkov (1951) and Kozlova (1957) list it as breeding sparingly on the Kamchatka Peninsula and Commander Islands and more commonly on the smaller Kuril Islands, the Shantar Islands, Sakhalin, the northern part of the Maritime Province, possibly on Russian Island near Vladisvostok, and south to northern Japan (Hokkaido and Honshu) and along the northeast and west coasts of Korea. The southernmost known breeding site is Ashi Island, off Kinkazan (Austin and Kuroda 1953).

The distribution and abundance of Common Puffins in the North Atlantic have changed drastically since the end of the last century (Cramp et al. 1974, Harris 1976a). Some colonies have been reduced to a fraction of their former size, others have disappeared altogether, and a few have increased.

The general breeding distribution for each of the subspecies of the Common Puffin is as follows (Figure 5d): F. a. grabae--the coasts

and associated islands of Scotland, England, Wales, Brittany, and southern Norway, and the Isle of Man, Channel Isles, and the Faroe Islands; F. a. arctica--the coasts and associated islands of western Greenland, Iceland, Northern Norway, Bear Island, Jan Meyen, Ainov Islands, Murmansk coast; and in North America, from approximately 55° N in Labrador south to New Brunswick and Machias Seal Island and Matinicus Rock, ME; F. a. naumanni--northwest Greenland (Thule area) south to about 60° N, eastern Greenland (Scoresby Sound?), Spitzbergen, and probably Novaya Zemlya (although the subspecies in this area is unclear) (Bent 1919, Salomonsen 1944, Dement'ev and Gladkov 1951, Kartashev 1960, Cramp et al. 1974, Lockley 1974).

Summer Distribution of Non-breeders

Since puffins of all four species do not breed until they are several years old, the question arises as to where the non-breeding populations occur. The presence of non-breeding adults and at least some of the older subadult birds at the breeding colonies has been documented for Tufted and Horned puffins (Wehle, Chapter 1; Sealy 1973b), Rhinoceros Auklets (Richardson 1961, Leschner 1976, Wilson 1977, and Summers and Drent 1979), and Common Puffins (Lockley 1953; Myrberget 1959, 1962; Corkhill 1972; Ashcroft 1976; Harris 1976b; Peterson 1977). Most authors, however, report that subadults at the colony arrive at various intervals after the breeding adults.

Pelagic observations conducted during the summer months have revealed that Tufted Puffins also occur on the open ocean throughout

this period (Jacques 1933; Kuroda 1955b, 1960; Hamilton 1958; Shuntov 1974; Bartonek and Gibson 1977; P. J. Gould, pers. comm.). The southern limit to the summer distribution of Tufted Puffins is apparently the Subarctic Front (Shuntov 1974).

During the summer months Horned Puffins are much less common on the open ocean than are Tufted Puffins (Jacques 1933, Arnold 1948, Kuroda 1955b, Hamilton 1958, Bartonek and Gibson 1977). The only report of Horned Puffins commonly sighted far from shore is in the Chukchi Sea at the northernmost limit of this species' breeding range (Swartz 1966). Hoffman et al. (1975) indicated that there has been a seasonal change in the pattern of observations of Horned Puffins off the west coast of the continental United States during this century. Whereas from 1914 to 1933 most of the records of Horned Puffins were made during the winter months, from 1953 to 1973, 20 of the 26 sightings of this species were made during the summer months. Reasons for this apparent shift in the behavior of Horned Puffins is unknown, but birds may be responding to long-term shifts in the atmosphere-ocean circulations of the North Pacific (Hoffman et al. 1975).

The farthest out to sea the Rhinoceros Auklet has been recorded during the summer has been approximately 29 km off Cape Flattery, WA, (Hamilton 1958). Apparently, the non-breeding population of this species remains within the coastal waters of its breeding range during the summer months.

Based on limited band recoveries, most non-breeding Common Puffins remain relatively close to either their natal or associated

breeding colony during the summer months (Mead 1974, Ashcroft 1976).

Thus, although at least some of the older subadults (3-4 yr old?) of each species are present on the breeding colonies for at least part of the breeding season, the remainder of the non-breeding population apparently summers at sea.

Winter Distribution

The true pelagic nature of puffins is revealed during the winter months and, as a result, our knowlege of their distribution at this time is poorly known. The fall-winter migration of the Tufted Puffins takes place mainly within the latitudes of its summer breeding distribution, with birds being thinly scattered over the great expanse of the North Pacific. The harsh winter environment of the Chukchi Sea, north Bering Sea, and Okhotsk Sea forces this species to migrate south into the North Pacific (Shuntov 1974). The northern distributional boundary is along a line passing from the southern Sakhalin headland along the Kuril Islands and from the southern coast of Kamchatka to the Commander Islands and through the southern part of the Bering Sea to the Pribilof Islands and the north coast of the Alaska Peninsula (Shuntov 1974). However, Shuntov (1974) indicated that the Tufted Puffin is scarce at the northern limit of its range in winter, a fact that has been more recently substantiated by P. J. Gould (pers. comm.). The southern boundary in winter appears to be approximately the same as that of summer, although some individuals may penetrate

slightly farther south (Gabrielson and Jewett 1970, Shuntov 1974).

Horned Puffins winter at sea from the limit of open water south (Gabrielson and Lincoln 1959), throughout the Aleutian chain (Murie 1959) and near the Commander and Kuril Islands south to North-central Honshu (Dement'ev and Gladkov 1951). Occasionally, they have been observed in winter at the Pribilof Islands (Preble and McAtee 1923). P. J. Gould (pers. comm.), however, reported very few Horned Puffins in the Bering Sea in winter.

On the west coast of North America, the Horned Puffin is a regular winter visitor to British Columbia, Washington, and Oregon, and casually to California (AOU 1957, Sealy and Nelson 1973, Hoffman et al. 1975). On the basis of pelagic observations and the occurrence of beached birds along the west coast of the U.S., Hoffman et al. (1975) suggested that Horned Puffins may winter over a wide range of latitudes in the Pacific and that there are likely to be a number of birds wintering at the latitudes off the west coast of the U.S. At this time, the southern boundary to the winter distribution of Horned Puffins has not been definitely delineated.

Rhinoceros Auklets are the least pelagic of the three Pacific puffins, both in summer and winter. Earlier published accounts indicated that Rhinoceros Auklets winter along the Asian coast from the southern portions of their breeding range, south to Japan and Korea, and along the North American coast to southern California and perhaps to Baja California (Bent 1919, Dement'ev and Gladkov 1951, AOU 1957, Kozlova 1957). However, our knowledge of breeding colonies at the

northern limits of their breeding range in the Gulf of Alaska and in the Aleutian Islands has increased greatly since the time of these writings. There is currently no evidence to suggest that birds breeding in these areas migrate to more southern coastal areas or that they are dispersed over the North Pacific during the winter months like Tufted and Horned puffins. I suggest that Rhinoceros Auklets breeding at these northern range limits probably also winter locally off these areas.

The winter distribution of three subspecies of the Common Puffin is as follows: F. a. grabae, especially those from the east coast of Britain, may winter in the waters of the North Sea near their breeding colonies, while those from the west coast may migrate south to the Bay of Biscay, Canary Islands, the Azores, and into the west Mediterranian Sea (Kartashev 1960, Cramp et al. 1974, Ashcroft 1976). Others may range far out to sea, being recorded up to 725 km offshore; and a few birds may even cross the Atlantic, as shown by three banded birds recovered off Newfoundland (Salomonsen 1944; Cramp et al 1974; M. P. Harris, pers. comm.). F. a. arctica apparently winters somewhat south of its breeding range, being found in the vicinity of the Faroe Islands and in the waters off Sweden and Denmark and rarely Germany (Salomensen 1944, Dement'ev and Gladkov 1951). In North America, birds winter from Baffin Bay at 77° N latitude (Welty 1975), south to southern New England and Long Island, NY, and east to the Grand Banks (Weber 1915, Tuck 1961). The northern subspecies, F. a. naumanni may, in mild winters, remain as far north as Amsterdam Island, North of Spitzbergen at 80° N latitude (Welty 1975), but

usually it ranges farther south, probably both near the coasts and on the open ocean. Greenland birds probably spend the winter in the waters of the Labrador Current (Salomonsen 1950).

Abundance

Sizes of puffin populations are difficult to obtain because of the birds' pelagic nature; their habit of breeding in concealed nests in remote, inaccessible areas; their irregular patterns of colony attendance; and their nocturnal activity (Rhinoceros Auklet). Hence, population estimates presented in Table 39 cannot be taken literally, but they provide orders of magnitude of abundance.

NESTING HABITAT

The resources for which competition in sympatric seabirds is most likely to occur are food and nest-sites (Ashmole 1963, Lack 1966, Carrick and Ingham 1967). Most colonial nidicolous seabirds, including alcids, nest in large colonies in relatively inaccessible sites, such as offshore islets, oceanic islands, and isolated promontories of the mainland coast (Lack 1968). Within the ranges of the puffin species, such sites are restricted, and the diversity of habitats within these sites is rather limited. Based on numerous published and unpublished descriptions of the nesting habitats of the puffin species, the relative frequencies for which the different major habitats are used by each puffin species are presented in Table 40. While the three Pacific

Table 39. Estimates of size of various puffin populations.

	Place	Estimated Population Size	Source
L. cirrhata	Alaska	c 4 million birds	1
	British Columbia	c 55,000 birds	2
	Washington	14,000-10,000 birds	3
	Oregon	?	
	California	c. 140 birds	4
	Asia	2-4 million birds (?)	
	TOTAL	6½-8 million birds	
F. corniculata	Alaska	1½ million birds	1
	Asia	1-2 million birds (?)	
	TOTAL	2-4 million birds	
C. monocerata	Alaska	c. 200,000 birds	1
	British Columbia	c. 140,000 birds	2
	Washington	c. 75,000 birds	3
	Oregon	200 birds	6
	California	c. 360 birds	4
	Asia	200,000-300,000 birds (?)	
	TOTAL	½-1 million birds	
F. a. grabae	Scotland	c. ½ million pairs	7
	Ireland	20,000-25,000 pairs	7
	England	c. 15,000 pairs	7
	Wales	8,000-10,000 pairs	7
	Isle of Man	c. 200 birds	7
	Channel Isles	c. 1,200 birds	7
	Brittany	400-450 pairs	7
	Southern Norway	c. 200 pairs	7
	Faroe Islands	400,000-1 million pairs	7
	TOTAL	2-3 million birds	
F. a. arctica	western Greenland	few thousand pairs	7
	Iceland	8-10 million birds	7
	Canada and United States	c. 1/3 million pairs	7
	north Norway	1¼ million pairs	7
	Bear Island	few hundred birds	7
	Jan Meyen	few hundred birds	7
	Russia	? 20,000 pairs	7
	TOTAL	10½-12½ million birds	
F. a. naumanni	northwest Greenland (Thule Area)	six small colonies	7
	eastern Greenland	very few	7
	Spitzbergen	5,000-10,000 birds	7
	Novaya Zemlya		
	[?] this race)	few	7
	TOTAL	15,000 birds	

sources: 1) Sowls, et al. 1978, 2) Vermeer 1976, 3) Frazer 1975, 4) G. J. Divoky, pers. comm. (for Farallone Islands), Ainley and Whitt 1973 (for rest of California), 5) Leschner 1976, Wilson 1977, 6) Scott et al., 1974, 7) Harris 1976b.

Table 40. The relative frequencies for which each major nesting habitat is used by the puffin species.

Habitat	Tufted Puffin	Horned Puffin	Rhinoceros Puffin	Common Puffin
Earthen burrows at cliff-edge	commonly	rarely	occasionally	commonly
Earthen burrows on seaslope	commonly	rarely	commonly (heavily vegetated)	commonly
Combination earthen burrow/rock crevice on seaslope or in vegetated talus slope	commonly	occasionally	occasionally	commonly
Rock crevices in talus slopes or under beach boulders	occasionally	commonly	rarely	commonly (at northern range limit)
Rock crevices in cliff-faces	rarely	commonly	never	rarely

sources: Tufted and Horned puffins; see Wehle, Chapter I. Rhinoceros Auklets; Heath (1915), Willett (1915), Kozlova (1957), Drent and Guiguet (1961), Richardson (1961), Leschner (1976), Wilson (1977). Common Puffin; see Nettleship (1972).

puffins differ in their preferences of nesting habitats, the habitats used by the Common Puffin are very similar to those of the Tufted Puffin. What evolutionary influences have acted to create these similarities and differences?

The ancestral puffin probably nested in burrows which it dug itself and possibly re-used in successive years. While Lunda and Cerorhinca remained in the Pacific Basin throughout their evolution, Fratercula immigrated via the Arctic Ocean to the Atlantic Ocean in the late Tertiary; it then spread back to the Pacific and became isolated into the high arctic Common Puffin (F. arctica) in the Atlantic and Horned Puffin (F. corniculata) in the Pacific (Udvardy 1963).

In the North Atlantic, Common Puffins could dig burrows, but Horned Puffins encountered habitat subject to permafrost. As a result of glaciations and other ensuing geoclimatic forces, numerous rock crevices became available in the form of talus slopes, rubble, and beach boulders. The interstices afforded by these piles of rock were probably not too dissimilar from the burrows Horned Puffins had used in the past, and thus, the birds were probably able to make the switch relatively easily, as indicated by the partial use of this habitat today by both Tufted Puffins and Common Puffins.

As the climate ameliorated, the southernmost limit of the Horned Puffin population again came into contact with unfrozen ground. However, competition for this habitat may have been acute, since it was already occupied by Tufted Puffins, Rhinoceros Auklets, and possibly Parakeet Auklets (Cyclorrhynchus psittacula), Cassin's Auklets (Ptychoramphus aleuticus), Ancient Murrelets (Synthliboramphus

antiquus), and Storm-Petrels (Oceanodrama spp.). Competition for areas suitable for burrowing may have restricted the southern movement of Horned Puffins and caused them to retain their habit of nesting in rock crevices.

In areas where both Horned and Tufted puffins nest in rock crevices, the former probably has the competitive advantage, owing to its smaller size and consequently greater accessibility to a larger number of potential nest-sites. In the several locations where Horned Puffins burrow today (see Wehle, Chapter I) other burrowing species are rare. Thus, the nesting distribution of Horned Puffins appears to be limited, in part, by the availability of rock crevices of suitable size.

Coupled with this historic distributional influence on the selection of Horned Puffin habitat is predation. Before man's arrival, most offshore islands inhabited by Horned Puffins were free from mammalian predators, although there were avian predators such as gulls and jaegers. While gulls may have occasionally taken adult Horned Puffins, most of their predation was probably on eggs and chicks. Both gulls and jaegers also probably engaged in aerial piracy (Ashmole 1971), and this form of predation may have had a major influence on the type of nesting habitats used by Horned Puffins.

Puffins have high wing-loading and are relatively poor fliers in that they lack maneuverability. Similarly, although they are able to walk and run better than most other alcids, they are still slow and awkward. Because of these handicaps, it is to their advantage to choose nest-sites which can be located easily and approached and left

rapidly. For Horned Puffins, rock crevices in talus areas, among beach boulders, and in cliff-faces fulfill these two needs. Within each of these habitats, the surrounding geomorphology of the area provides numerous landmarks to aid in immediate location of the nest-site and the angle of slope and the presence of numerous pinnacles allows for rapid landings and take-offs.

The characteristics determining the suitability of potential nest-sites for Tufted and Common puffins are the same: soil depth, distance to the cliff-edge, and/or the angle of slope. Soil depth is important as it allows the bird to re-use the burrow in successive years without having to expend time and energy digging a new one or making substantial repairs on an old one. The importance of distance to the cliff-edge and the angle of slope is related to the predation pressure imposed by avian pirates. The closer the burrow to the cliff-edge, and the greater the angle of slope in which the burrow is located, the easier it is for the birds to land and take off quickly. The time-saving element involved with both of these habitats is further increased by the nature of the habitat serving as a landmark.

Suitability of nest-sites for Rhinoceros Auklets is determined by soil depth, the angle of slope, and the degree of vegetative cover. The importance of soil depth is the same as that discussed for Tufted and Common Puffins. The other two factors are apparently again related to potential aerial avian predation. However, Rhinoceros Auklets tend to select habitats in which these characteristics are different than those selected by Tufted and Common puffins. Rhinoceros Auklets prefer gradual slopes, usually with heavy vegetation.

The differences in habitat preferences between Rhinoceros Auklets and Tufted and Common puffins may be related to differences in the activity patterns of diurnal Tufted and Common puffins versus nocturnal Rhinoceros Auklets. Nocturnal activity by the auklets avoids predation or piracy by gulls during the feeding of chicks (Lack 1966, Cody 1973). Then why does nocturnal activity lead to dissimilar characteristics in nest-sites from those of the diurnal puffins? As aerial predators do not hunt at night, steep slopes are not needed by Rhinoceros Auklets. Further, because the auklets suffer from relatively high wing-loading and poor maneuverability, gradual slopes may provide an easier place to land in the dark than steep slopes. It is also likely that Rhinoceros Auklets have a more difficult time locating their burrows in the dark, and a gradual slope affords them the opportunity to land in the general vicinity of their burrow and walk to the burrow site, a luxury diurnal puffins cannot afford.

The preference of Rhinoceros Auklets for slopes with a dense vegetative cover has been attributed to the fact that the vegetation prevents erosion and prolongs the life of the burrows (Richardson 1961, Leschner 1976, Wilson 1977). I suspect this factor is secondary and suggest that the primary reason is the lack of nocturnal aerial predators which allows Rhinoceros Auklets to safely walk a considerable distance from an open landing spot, through the vegetation, to their burrows. Thus, Rhinoceros Auklets are able to use a habitat that is unsuitable for Tufted Puffins due to the increased predation pressure imposed by the latter species' diurnal habits.

A reversal of activity patterns, from nocturnal to diurnal, has been reported for Rhinoceros Auklets at three sites: Sea Lion Caves and Goat Island, OR, and South Farallon Island, CA, (Scott et al. 1974). This diurnal activity has been observed only where Western Gulls (Larus occidentalis) and not the somewhat larger Glaucous-winged Gull (Larus glaucescens) breed (Scott et al. 1974). However, in these areas there is almost a complete overlap in the size between these two gull species thus leading Scott et all (1974) to conclude that some factor other than predator size is responsible for the observed differences in Rhinoceros Auklet nocturnal/diurnal activity patterns. A partial answer to this problem may be found in the type of nesting habitat the birds use.

At Sea Lion Caves, where the birds nest inside the caves, potential harassment by gulls is reduced by the auklets approaching their nest-sites directly from the sea below the gull colony and by the gulls' reluctance to enter the dark interior of the caves (Scott et al. 1974). Thus, largely freed from potential predation by gulls, the auklets have become diurnal. Similar habitats farther north are not used by Rhinoceros Auklets, possibly as a result of competitive exclusion by Horned Puffins.

On South Farallon Island, populations of Rhinoceros Auklets and Tufted Puffins are only a small fraction of their former size (Ainley and Lewis 1974). Hence, competition between these two species for nest-sites is probably not keen. In the absence of such competition, Rhinoceros Auklets are able to occupy nest-sites in areas which are not heavily vegetated and which allow for rapid take-offs and landings

(D. G. Ainley, pers. comm.), thus favoring diurnal activity. Similarly, the small population sizes of Rhinoceros Auklets and Tufted Puffins on Goat Island (Browning and English 1968, Bartonek and Sowl 1972, Scott et al. 1974) suggest that competition between these two species for nest-sites is probably minimal and that Rhinoceros Auklets are able to nest in habitats which allow diurnal activity.

THE PRE-EGG STAGE

Arrival and Settlement

The arrival and settlement of all puffin species at the breeding colony is characterized by the same four events observed in Tufted and Horned puffins (Wehle, Chapter I): first arrival, first land-coming, establishment of continuous occupancy, and the initiation of egg-laying. Arrival of individuals within each of the four species at the breeding colony tends to be synchronous, with scattered individuals appearing offshore usually only several days before the population arrives en masse. Similarly, a few birds may appear on land at irregular intervals after arrival, but first land-coming tends to involve most of the population first visiting the colony on the same day. Some species of puffins are present at or in the vicinity of the colony in a quasi-cyclical fashion (Nettleship 1972) during all or part of the pre-egg stage before they establish continuous occupancy; after which, at least a substantial part of the population remains at or in the vicinity of the colony.

For each puffin species, there is a positive correlation between the time of arrival and latitude, with birds arriving earlier at the southern limits of their range (Appendix I). The variation in arrival times between the northern and southern limits of breeding distribution ranges between 2 and 3 mo for Tufted Puffins, 1 and 2 mo for Horned Puffins, probably 1 and 2 mo for Rhinoceros Auklets (accurate arrival times in the north are lacking), and about 1 mo for Common Puffins. Most authors attribute this latitudinal variation in arrival time to variations in sea and to nesting habitat conditions. Later arrival results from lingering ice in the seas, and from the presence of snow cover, ice, or otherwise unfavorable conditions on the breeding colonies (Dement'ev and Gladkov 1951, Belop'skii 1957, Kozlova 1957, Uspenski 1958, Kartashev 1960, Sealy 1973b).

The pattern of colony settlement shows considerable variation among the four species of puffins (Appendix II). The interval between arrival and first land-coming for Tufted and Common puffins is usually between 1 and 2 weeks, while that of Horned Puffins is less than 1 week.

Tufted and Common puffins, and probably also Rhinoceros Auklets, do not establish continuous occupancy for several weeks after their arrival, during which time their numbers on or in the vicinity of the colony may vary by a factor of a thousand on any given day. Horned Puffins on the other hand, establish continuous occupancy shortly after their arrival, after which they are present on or in the vicinity of the colony in relatively stable numbers. The interval between first land-coming and continuous occupancy is also several

weeks for Tufted and Common puffins, but these two events usually coincide for Horned Puffins.

In many cases, the establishment of continuous occupancy and the onset of egg-laying are simultaneous for Tufted and Common puffins, but these events are usually separated by a 2- to 3-week interval in Horned Puffins. The interval between first land-coming and the commencement of egg-laying is approximately a week shorter for Tufted and Common puffins than for Horned Puffins.

Finally, the length of the pre-egg stage, from first arrival to the onset of egg-laying, appears to be strongly correlated with latitude for Tufted Puffins but less so for Horned Puffins, Rhinoceros Auklets, or Common Puffins (Appendix II). The length of this interval is nearly twice as long for Tufted Puffins at the southern than northern limits of their range. At the same latitude, the length of the pre-egg stage is slightly longer for Tufted than Horned puffins, and it is generally shorter for Tufted and Horned puffins than for Rhinoceros Auklets and Common Puffins.

Before examining some possible explanations for these similarities and differences, a brief mention of the attendance patterns of these birds at the colonies is in order. Cyclic patterns of attendance at or in the vicinity of the colony during the pre-egg stage occur in Tufted Puffins but not Horned Puffins (Wehle, Chapter I). For Rhinoceros Auklets, Leschner (1976) mentioned sporadic periods of colony attendance during the pre-egg stage, and Wilson (1977) noted periods of absence between visits to individual burrows of this species from 6 to 35 days. Descriptions of a cyclic pattern of attendance for Common

Puffins during this stage include: three or four periods of a 2-7 day cycle (Lockley 1934), five periods of a 3-7 day (mean 5.2 days) cycle (Corkhill 1971), and four periods of a several day cycle (Nettleship 1972). In addition, Myrberget (1955) and Lloyd (1972) mentioned the occurrence of a cyclic pattern of attendance by Common Puffins but did not indicate the length and the cycles observed.

Possible explanations for irregular or cyclic patterns of attendance during the pre-egg stage of certain puffin species include weather (Perry 1946, Myrberget 1959, and Corkhill 1971); social stimulation (Corkhill 1971); day length (Lloyd 1972); sea temperature (Lloyd 1972); and the arrival of first-time, inexperienced breeders (Frazer 1975). However, all of these explanations fail to account for the observed rhythm of the attendance patterns and for the fact that in areas where Tufted and Horned puffins are sympatric, only the Tufted Puffin exhibits these cyclic patterns of attendance.

Equivalent absences during the pre-egg stage has been reported in alcids only for the Ancient Murrelet (Sealy 1972), but occurs in a number of Procellariiformes (Marshall and Serventy 1956; Davis 1957; Maher 1962; Tickell 1962; Dunnett et al. 1963; Harris 1966, 1969, 1970; Lack 1966). The generally accepted function of this "honeymoon" (a period of feeding after copulation) is for both sexes to replenish expended food reserves and for females to obtain sufficient energy reserves necessary for the formation of the egg (Ashmole 1963, 1971; Lack 1966, 1967; Harris 1969; Perrins 1970; Sealy 1972).

Even though puffins may spend considerable time in rafts in the vicinity of the colony, they apparently do not feed (Lockley 1934,

1953; Amaral 1977; Wehle, Chapter I), presumably because of insufficient nearshore food resources at that time. Hence, the birds are probably forced to travel a considerable distance to more productive feeding grounds (Lockley 1934). The rhythm imposed on these periodic absences from the colony area has been interpreted as hunger superseding sexual instinct (Lockley 1934). However, the observed variation in rhythm of these cycles could be influenced by any number of the previously mentioned factors.

The question still remains as to why Horned Puffins do not exhibit the same cyclic pattern of attendance during the pre-egg stage as shown by the other three puffin species. If food-related factors are primarily responsible for the cyclic patterns displayed by three of the puffin species, then it is logical to assume that food-related factors also may be responsible for the Horned Puffins not showing these cyclic patterns of attendance.

In areas of sympatry, Horned Puffins tend to be inshore feeders, foraging considerably closer to shore than Tufted Puffins (Willett 1915; Sealy 1973b; Hunt 1977; Wehle, Chapter I), and, in general, the distance to foraging areas of Horned Puffins is less than those reported for the other three puffin species (Heath 1915; Willett 1915; Witherby et al. 1941; Kozlova 1957; Richardson 1961; Pearson 1968; Cody 1973; Corkhill 1973; Ashcroft 1976; Dick et al. 1976).

This predilection for inshore feeding may have evolved in response to the limited open water present along the coasts during the height of glaciation, when Horned Puffins were restricted to a more northerly distribution than either of its two Pacific relatives. Later,

when the ranges of these species overlapped, it is possible that Horned Puffins were able to competitively exclude the other two puffins from this nearshore zone. The mechanics, however, of such competitive exclusion remain unclear. Similarly, in the Atlantic, the Common Puffin may also have been excluded from feeding in nearshore waters by other sympatric species. Although this hypothesis remains speculation, Horned Puffins do not exhibit the cyclic pattern of colony attendance shown by the other three puffin species. They feed in the nearshore waters during the breeding season. Thus, they do not require periodic long-distance flights to obtain food.

Much of the similarity in pattern of colony settlement between Tufted and Common puffins, and the difference between these two species and Horned Puffins is related to their patterns of colony attendance. Tufted and Common puffins do not establish continuous occupancy until close to or concomittant with the onset of egg-laying. Each of these species engage in cyclic absences from the colony during the pre-egg stage during which time they travel to distant foraging areas for the purpose of obtaining food. Horned Puffins, on the other hand, establish continuous occupancy soon after arrival as a result of their being able to feed in the nearshore waters of their breeding colony.

The interval between arrival and first land-coming is usually slightly longer for Tufted and Common puffins than Horned Puffins as the result of the former two species possibly making at least one mass exodus from the vicinity of the breeding colony prior to their first

return to land. However, there is considerable variation in the length of this interval between colonies. This variation, in turn, may be the result of variations in feeding conditions encountered by the birds prior to their first arrival at different locations or in different years.

Finally, the length of the pre-egg stage of the puffins is determined primarily by two factors. First, arrival times are directly related to the accessibility of nest-sites as determined by climatic factors. The importance of these climatic factors, e.g., ice, snow, and water conditions, are especially acute in the northern portions of the species' ranges. Second, the breeding seasons of seabirds have evolved so that the timing of egg-laying is such as to maximize the potential of producing young that survive to breeding age (Carrick and Ingham 1967, Lack 1968). The main selective force determining this optimal time for egg-laying is the availability of food, whether it be to provide sufficient energy reserves for the production of an egg(s) by the female, or to meet the demands of the growing young (Pitelka 1959; Holmes 1966, 1971; Lack 1966, 1968 and others). Thus, variation in the length of the pre-egg stage with latitude for each of the puffin species reflects the interaction of these two factors; food availability probably being more important at the southern limits and nest-site accessibility probably more important at the northern limits of their breeding distribution. Although there are a number of exceptions, the length of the pre-egg stage for Tufted and Horned puffins is generally shorter than for Rhinoceros Auklets and Common Puffins.

This is probably due to the fact that throughout much of the breeding range of the former two species, the two controlling factors (accessibility of nest-sites and timing of egg-laying related to food availability) coincide to a greater extent than they do in the more southerly regions of the Pacific or in the Atlantic, where the latter two species breed.

Behavior

Sexual Behavior

The sexes of all four puffin species are monomorphic, although males tend to be slightly larger than females. Prior to their arrival at breeding colonies in spring, each species undergoes an incomplete prenuptial molt which provides them with adornments apparently important only for courtship (Bent 1919, Dement'ev and Gladkov 1951, Kozlova 1957, Harris and Yule 1977). It is not surprising therefore, that the puffins accentuate these adornments in their sexual behavior.

Courtship Ceremony Leading to Copulation.--Courtship behavior and copulation in Tufted, Horned, and Common puffins occurs as soon as the birds arrive at the colonies, but it is unclear whether this is a continuation of events begun while the birds were still at sea.

The courtship ceremony of these three species appears similar (Lockley 1934, 1953; Witherby et al. 1941; Perry 1948; Salomonsen 1950; Myrberget 1962; Frazer 1975; Amaral 1977; Wehle, Chapter I);

courtship behavior of Rhinoceros Auklets has not been described. The general sequence of courtship events is as follows: members of a courting pair tend to swim in close proximity to each other within a nearshore raft of birds. As the male follows behind the female, usually by several meters, he repeatedly jerks his head up and down, opening his mandibles on the upstroke and closing them on the downstroke. This activity may continue for several minutes during which time the female may also, though infrequently, engage in head-jerking. Vocalizations probably accompany head-jerking by the male (Salomonsen 1950; Lockley 1953; Wehle, Chapter I). If the female is interested in mating she slows down, allowing the male to approach her from behind. With a rapid fluttering of his wings, he alights on her back, immersing her completely in the water except for her head. During coition, the male continues to vigorously flap his wings to maintain his position. Copulation generally lasts less than a minute and is usually terminated by the female diving out from under the male and resurfacing several meters away. At this point one or usually both birds wing-flap and/or preen (see below). Other displays, especially billing and bill-gaping may be interspersed at any time during the ceremony. Courtship frequently attracts nearby birds which attempt to "participate", resulting in unsuccessful coition of the original pair.

Apparently, Common Puffins sometimes attempt copulation on land, but such attempts are usually not successful (Perry 1948; Conder 1950; Lockley 1953, 1954; Kartashev 1960; Myrberget 1962; Ashcroft 1976).

Billing.--In all four puffin species, billing occurs in the water, especially during the pre-egg stage, and on land, throughout the breeding season, but it is much more common in the earlier than later breeding stages. Either sex may initiate billing, but in most cases it is probably the male.

The postures of the two birds during a bout of billing varies. On water, both birds usually assume a low profile with their necks outstretched. On land, one bird usually stands erect, with its nape and breast feathers fluffed out and its head lowered. The other bird initiating the bout is usually crouched low to the ground with its feathers sleeked and its head raised slightly upward. On both land and water, one, both, or neither bird may have its tail raised above the wing tips. The initiating bird usually begins by gently nuzzling the throat and breast feathers of the other. It then brings its bill up under the bill of the other bird while swinging the head from side to side. At this point, both birds position their bills so as to lie broadside against each other. The birds then move their heads from side to side with their bills separating from each other momentarily before being slapped together. The sound produced when the bills make contact is similar to that of two plastic rules being slapped against each other. Under favorable conditions the sound can be heard 15-20 m away (Myrberget 1962). Bouts last from a few seconds to several minutes and may be repeated several times per hour.

Billing is frequently observed after one bird lands near its mate on the colony, prior to the entry of a pair into a nest-site, after an aggressive action of one member of the pair towards another bird,

after a gull-alarm disturbance, after head-jerking, after a bowed-head display, or during the courtship ceremony. However, observations of this behavior in other situations indicate that billing, or at least the initial movements leading toward billing, may have broader implications. Subadult birds, apparently arriving on the colony for the first time, will attempt to bill with established breeders, perhaps to test for friendliness or to ascertain the sex of the other bird (Lockley 1934).

Billing or its precursory movements may have been evolutionarily related to feeding as suggested by my observations of a single Horned Puffin adult going through the motions of billing when delivering the first bill-load of food to its chick and by both captive Tufted and Horned puffin chicks going through similar motions when offered food from my hand (Wehle, Chapter I). Similarly, nestling Common Puffins frequently emerge from their nest-sites to bill with their parents (Perry 1948; M.P. Harris, pers. comm.).

Billing is contagious and, typically, nearby birds will approach and attempt to participate with a billing pair. Such group stimulation in other species of birds has been found to enhance the synchrony of breeding activities (Hickling 1959, Brown and Baird 1965, Immelmann 1971).

Head-jerking.--Head-jerking involves a bird throwing its head up and back to the farthest extremes of its vertical range of motion. This behavior has been described for Tufted and Horned puffins (Wehle, Chapter I) and for Common Puffins (Bent 1919, Perry 1940, Conder

1950, Lockely 1953, Myrberget 1962, Nettleship 1972, Taylor 1976). All three of these puffin species use this display as a part of the courtship ceremony, but it appears only limited to that context in the Tufted Puffins.

Myberget (1962) described two forms of head-jerking (head-nodding) for Common Puffins: sexual nodding and social nodding. Sexual nodding is used by the male as an invitation for mating. When the male is at his highest peak of excitement, his bill may point straight upwards. On land, this behavior is apparently only directed toward its own mate, but on the water, one male may display to several females in turn. Social nodding occurs only on land and is less intense than sexual nodding, the bill swinging less rapidly and to only 45° to 60° above the horizontal. Like a number of other puffin behaviors, social nodding is contagious, with varying numbers of birds participating at the same time. Although Perry (1940) contended that probably only males engage in social nodding, Conder (1950) and K. Taylor (pers. comm.) suggested that females probably also participate. I believe female participation is also the case in Horned Puffins.

Apart from social nodding, which usually involves a group of birds, head-jerking has been observed in individual Horned and Common puffins under other circumstances: by a male defending a female from intruders and by an intruder after being driven off by a presumed male (Conder 1950), prior to billing (Wehle, Chapter I), after billing (Lockley 1953), and after an incoming bird alights near birds already in situ (Perry 1940).

The function of head-jerking has been considered partly sexual, partly bellicose (Perry 1940), a threat display used to defend a territory (Nettleship 1972), and an appeasing action (Lockley 1953). My observations suggest that head-jerking serves an appeasement function.

Bowed-head Display.--This display has been observed in Tufted Puffins (Wehle, Chapter I), Rhinoceros Auklets (L. L. Leschner, pers. comm.), and Common Puffins (Salomonsen 1950, Lockley 1953, Myrberget 1962). The bird holds its body low and horizontal to the ground and tilts its head down so that the tip of its mandibles nearly touches its feet. In Common Puffins and Rhinoceros Auklets, the head remains in a fixed position, but in Tufted Puffins the head is sometimes swung slowly from side to side. While I have observed Tufted Puffins executing this behavior only on land, Common Puffins apparently do it both on land and on water (where the bill is held down to the water surface). Rhinoceros Auklets perform this display only on water.

The apparent functions of this display in Tufted Puffins are to entice a mate into a nest-site, to invite billing, or as an aggressive display. In Common Puffins, it may also indicate a desire to bill (Myrberget 1962) or it may be an aggressive display (Lockley 1953). The context in which it was observed in Rhinoceros Auklets made its function unclear (L. L. Leschner, pers. comm.).

Social Behavior

The social behaviors discussed below include those behaviors, other than sexual, which directly relate to potential or actual encounters between puffins. Territoriality of puffins, which may involve a number of social behaviors, is also discussed.

Fly-bys.--Puffins engage in repeated circular flights over the breeding colony and adjacent water before the birds resettle in the nearshore rafts or land on the colony. Although numerous other functions have been ascribed to this behavior (Lockley 1953, Richardson 1961, Skokova 1962, Corkhill 1971, Amaral 1977), its primary importance is probably related to predator avoidance and/or social stimulation (Grant 1971; Amaral 1977, K. Taylor, pers. comm.).

Landing Display.--Tufted, Horned, and Common puffins execute this display immediately after landing on the colony (Taylor 1976; Wehle, Chapter I). The bird holds its body low and horizontal to the ground, and the wings are held above the back and usually outstretched distally from the humerus. The head may be outstretched horizontally in line with the body, but more typically in Tufted and Horned puffins, it is held to varying degrees downward. In the Common Puffin the head is normally held up. In this position the bird may take several exaggerated steps forward ("forward stomping" of Taylor 1976), before slowly closing the wings and assuming a normal posture. The duration of the display in all three species is positively correlated with the number

and negatively correlated with the proximity of birds in the immediate vicinity of the landing, i.e., the greater the number and the shorter the distance to birds already present the longer the display. An appeasement function of this display is suggested by Taylor (1976), who observed that inexperienced 2-year-old birds landing on the colony did not hold the display long enough and thus were attacked or gape-threatened by birds standing nearby. This display has probably become ritualized from an original function of balancing or coping with the shock of impact upon landing (Taylor 1976).

Bill-gaping.--Bill-gaping is probably the most important threat display of Tufted, Horned and Common puffins (Lockley 1953; Myrberget 1962; Nettleship 1972; Amaral 1976; Taylor 1976; Wehle, Chapter I). When bill-gaping, the bird stands erect with neck stretched upwards and the bill facing the recipient of the threat. The neck and head feathers are ruffled, and, in Tufted Puffins, the plumes are raised. The mandibles are held widely apart, exposing the brightly colored linings of the mouth, and the tongue may or may not protrude. This display is sometimes accompanied by a vocalization (Lockley 1953; Z. Eppley, pers. comm.).

Bill-gaping is differentiated from the yawning of weariness by the feathers not being ruffled, the tongue not protruding, and by no vocalization during yawning. Typically, the yawn also has a much shorter duration.

The length of time of bill-gaping appears positively correlated with the seriousness of the threat, although it generally lasts less

than 5 sec. The threat is usually in response to an intrusion by a bird into another puffin's territory; following the landing of another bird on the colony; before, during, and after a fight; by unwilling partners during the courtship ceremony; and by one or both members of a pair when a third bird attempts to join their billing.

Fighting.--Fighting occurs in all four species and is usually caused by the trespassing of one bird on another's territory or from the intrusion of a third bird while a pair is billing. In most cases, the male probably starts the fight. Physical combat is usually preceded by warnings in the form of bill-gaping, feather ruffling, plume erection (Tufted Puffins), and/or aggressive bowing. Most battles end with little damage to either of the participants. Frequently, spectators will surround two fighting birds, and occasionally the fight is terminated by the intrusion of a third bird. However, I have never witnessed more than two birds involved in a fight.

Territoriality.--Nest-site establishment is probably accomplished by territorial antagonistic behavior among males in Tufted Puffins (Wehle, Chapter I), Rhinoceros Auklets (Richardson 1961, L. L. Leschner, pers. comm.), and Common Puffins (Perry 1940, Lockley 1953, Grant and Nettleship 1971, Nettleship 1972, Ashcroft 1976). That territoriality has not been documented for Horned Puffins is probably due to the nature of their hidden nest-sites. Apparently, Horned Puffins defend the area in the immediate vicinity of their nest (Wehle, Chapter I).

For Tufted and Common puffins, and probably Rhinoceros Auklets, the area defended usually includes the burrow (or actual nest-site) and its entrance, the approach path to the burrow, and a specific raised area in the immediate vicinity of the burrow which is used for taking off and landing and as a resting place when the birds are on colony. This latter area may consist of a grass hummock, a mound of earth, or a projecting rock surface.

In general, territories of all puffin species have a radius of less than 1 m from the burrow or nest-site entrance, but the size probably varies with burrow density. In many areas, a stretch of "no-man's-land" exists between territories. Puffins defend their territories by head-bowing, bill-gaping, and/or physical combat. Physical presence alone is important, as territorial trespassing is common when the owners are away from the colony. Defense of a territory is most keen during the pre-egg and egg-laying stages, becoming gradually less frequent throughout the rest of the breeding season.

Body-care Behavior

All four species of puffins perform three common behaviors which are related to the maintenance of normal body function: head-dipping, wing-flapping, and preening.

Head-dipping.--This behavior, performed only on the water, consists of a bird lowering its head into the water to just above the eyes for a couple of seconds; it may be repeated a number of times in succession.

Head-dipping occurs in all four puffin species under a wide variety of circumstances, and appears to be primarily a comfort behavior, perhaps serving the function of keeping the eyes moist. Sometimes, however, it may be used as a flight intention movement (K. Taylor, pers. comm.). Z. Eppley (pers. comm.) observed a Tufted Puffin in captivity attempting to vocalize while head-dipping.

Wing-flapping.--Wing-flapping is characteristic of most waterbirds and is performed both on land and water. In this behavior the bird assumes an erect posture, fluffing out the feathers of the entire body, and beating its wings several times. Its apparent function is to dislodge water from and/or replenish the supply of trapped air in the feathers. However, it may also be used as a displacement activity, and/or a flight intention movement (K. Taylor, pers. comm.). This behavior is particularly infectious among birds in close proximity.

Preening.--Puffins preen both on the water and on land. The broadside of the bill is repeatedly rubbed on the uropygial gland and the secretion then smeared over the feathers. Individual primaries and retrices are drawn through the tip of the bill. Preening serves the function of waterproofing, feather maintenance, and removal of ectoparasites.

Vocalizations

Puffins are not as vocal as some other alcids, e.g., murres and auklets. They do, however, have a limited repertoire of vocalizations which probably serve a communicative function--though in most cases the meanings are not clear.

Tufted and Horned puffins have four general vocalizations in common, three of which show some interspecific variation (Wehle, Chapter I). Each of these four vocalizations resemble, at least superficially, vocalizations reported for Common Puffins. Although published descriptions of the vocalizations of Rhinoceros Auklets are few, this species appears to have at least two vocalizations that are similar to those of the other three species (Table 41).

All four puffins have a short, sharp, intense call which appears to serve primarily as a threat. Tufted, Horned, and Common puffins all share a "purring call" which is similar to the threat call, but lasts several seconds longer. It is a low-pitched "err," but much softer in intensity than the threat call; it has the low purring quality of a cat. These three species also have a bi-syllabic call, characterized by a short, sharp, and intense vocal "er", followed immediately by a second syllable initiated by a higher pitched call note. Finally, all four puffins have a long, multi-note call consisting of at least three syllables, with the third syllable frequently repeated many times.

Table 41. Comparative vocalizations of puffins.

Type of Vocalization	Tufted Puffin[1]	Horned Puffin[1]	Rhinoceros Auklet	Common Puffin
Threat call	short vocal errr	short vocal errr	"single, low notes"[2]	"a short harsh urrr"[4]
Purring call	long errr (repeated)	long errr (not repeated)		"deep purring arrr"[5]
Bi-syllabic	ér errr	ér errr (undulating pitch on 2nd syllable)		"co-o-or-aa" "haa-haa"[6]
Long multi-note call	ér↑errr↓↑errr↓ ↑errr↓↑errr↓ (siren call)	ér↑errr↓ ér er er er (er)	4-7 note call[3]	"Haa-aa...aa-aa aa-aa-aa[7]

↑ indicates rise in pitch
↓ indicates decrease in pitch
ˊ indicates primary stress
° indicates secondary stress

sources: 1) Wehle, Chapter I; 2) Richardson 1961; 3) Heath 1915, Kozlova 1957, Richardson 1961; 4) Perry 1940; 5) Cramp et al. 1974; 6) Lockley 1953; 7) Perry 1940.

Nest-site Preparation

The degree of nest-site preparation required in the various puffin species depends on the type of nesting habitat. For Tufted and Common puffins and Rhinoceros Auklets, which typically nest in earthen burrows, the task is greater than for Horned Puffins, which typically nest in rock crevices. Birds clean both types of nest-sites before gathering fresh nesting material and building a new nest, but the burrow-nesters often need to make repairs to the burrow.

Although Tufted and Common puffins and Rhinoceros Auklets have been reported to dig new burrows during the pre-egg stage, most of these burrows are not used within that same breeding season (Frazer 1975; Richardson 1961; Lockley 1953, 1954, Uspenski 1958). Apparently there is insufficient time (or energy) to excavate a new burrow during the pre-egg stage and complete the breeding cycle in the same season. Most digging of new burrows takes place in the late incubation or nestling stages, presumably by subadult birds or by birds who have lost or deserted their original burrows (Lockley 1953, 1954; Richardson 1961; Leschner 1976; M. J. Amaral, pers. comm.; Wehle, Chapter I). Consequently, each spring most puffins occupy burrows already present.

Early preparation of the nest-site centers on burrow repair and cleaning. The life expectancy of burrows varies in relation to physical conditions of the soil (e.g., particle size), climate-related factors (e.g., frost-heaving), vegetative cover (related to erosion), the presence of other animals (particularly trampling by mammals), and

other environmental factors. During the winter months, many earthen burrows are damaged by ice, snow, and rain. In addition, burrows may be inhabited during winter by other animals (mice, rabbits, etc.) which leave debris when they depart in the spring.

If structural damage to the burrow is considerable, the burrow may be enlarged during the pre-egg stage. Excavation of burrows is done in a similar fashion by the three burrow-nesting puffins. The bird uses its bill as a pick-axe and wedge to chip away small pieces of substrate, and then it pushes the loosened soil out of the burrow with a backward scraping motion of the feet. This simple technique can result in burrows up to 15 m long (Kartashev 1960) and in the removal of objects (e.g., rocks) over twice the bird's own weight (Wehle, Chapter I). For Common Puffins, Bent (1919) states that excavation is done chiefly by the male, but Belopol'skii (1957) contends that it is done by both sexes.

Tufted Puffin burrows which remained structurally sound over the winter and Horned Puffin nest-sites which are largely free of destructive environmental forces during this period are usually cleaned of debris each spring by the same backward scraping motion of the feet.

Nests of all puffin species typically vary considerably in size. The most common nesting materials for all species are grasses and flight feathers of puffins and gulls. These materials may be supplemented with mosses, ferns, seaweed, woody twigs, leaves, stones, and fishing line.

Nesting material is usually collected in the immediate vicinity of the nest-site, but in areas where it is not locally available, birds may

fly to other areas (of the island) to secure it (Drent and Guiguet 1961, Amaral 1976). In Tufted and Common puffins, both sexes participate in collecting nesting material (Perry 1940; Wehle, Chapter I).

Nest-site Tenacity

Nest-site tenacity has been demonstrated in Tufted Puffins (Wehle, Chapter I), Rhinoceros Auklets (Richardson 1961, Leschner 1976), and Common Puffins (Lockley 1953; Skokova 1962; Nettleship 1972; Ashcroft 1976; and M. P. Harris, pers. comm.).

At least 29% of the Tufted Puffins I have monitored exhibited nest-site tenacity (Wehle, Chapter I). Similarly, at least 36% (Leschner 1976) and 50% (Richardson 1961) of Rhinoceros Auklets returned to the same nest-site in successive years. Ashcroft (1976) found that 95% of the Common Puffins she studied retained their nest-sites from one year to the next, and she observed no difference in nest-site tenacity between sexes; at least half of the observed changes in Common Puffin nest-sites were due to the eviction of the occupants by other birds (usually other puffins, but sometimes shearwaters).

Although nest-site tenacity has not been demonstrated for Horned Puffins, there is some circumstantial evidence to suggest its occurrence. I have observed a number of Horned Puffin nests located in exactly the same location in talus slopes and under beach boulders in successive years (Wehle, Chapter I). Similarly, Sealy (1973b) found that Tufted and Horned puffins returned to their snow-covered nesting slopes and landed on top of the snow over their future nest-sites,

thus suggesting some prior familiarity with their location.

Lack (1954) indicated that nest-site tenacity was positively correlated with breeding success. In puffins, enhanced breeding success through nest-site tenacity apparently works in conjunction with two other factors: the relative shortness of the breeding season and intraspecific competition for nest sites.

Throughout much of their ranges, puffins arrive at their nest-sites earlier than they are able to occupy them due to climate-related factors (e.g., ice, snow, or water over, or in the nest-sites). Familiarity with the location of one's nest-site even when buried under snow (see Sealy 1973b, 1975), would facilitate its occupancy as soon as it became available--an ability that may be important in an environment where time is a crucial factor (Bedard 1969, Sealy 1975). These same factors (familiarity with the location of one's previous nest-site and the tendency to re-occupy it) would also reduce intraspecific competition for nest-sites and thereby conserve time and energy.

Thus, those birds which are able to occupy their nest-sites earliest and minimize potential competition as a result of nest-site tenacity apparently have a reproductive advantage over those which do not. Hence, selection favors the perpetuation of nest-site tenacity in these species. Nest-site tenacity also probably aids in reuniting members of a pair which presumably have been separated during the winter. This function may also explain why the interval between first arrival and first land-coming is relatively short.

Nest-site Competition and Cohabitation

The potential for interspecific competition encountered by each puffin species varies from colony to colony in response to: the number and abundance of other sympatric species which may compete for the same nest-sites, and, the availability of suitable nest-sites.

In this section, I have identified those species, both avian and mammalian, which cohabit nest-sites with puffins. Cohabitation of nest-sites may not involve interspecific competition but rather may be an extreme example of ecological segregation in an environment where availability of nest-sites may be the most important factor determining species diversity and abundance at a specific colony.

Fork-tailed and Leach's storm-petrels are the most commonly reported species to share burrows with Tufted Puffins (Frazer 1975; Wehle, Chapter I). In most cases, Tufted Puffins nested in the large chamber at the far end of the burrow, while the storm-petrels nested in small side-tunnels or recesses near the entrance of the burrow. Presumably, this selection of different sites within the burrow reduced interaction between the species.

Frazer (1975) observed several instances of Tufted Puffins and Rhinoceros Auklets nesting in the same burrow. Sometimes both species occupied the same tunnel, and sometimes the Rhinoceros Auklets nested in short side tunnels. In at least one of these burrows, both species managed to successfully raise their chick.

Other bird species found cohabiting the same burrow with Tufted Puffins have been Ancient Murrelets (Synthliboramphus antiquus) and Parakeet Auklets (Cyclorrhunchus psittacula) (Wehle, Chapter I).

On the Farallon Islands, CA, Ray (1904) reported confrontations of Tufted Puffins with European Rabbits (Oryctolagus cuniculus) within burrows, but indicated that the puffins were usually able to usurp the territory occupied by the rabbits.

Because of the inaccessible locations of most Horned Puffin nest-sites, there are few reports of cohabitation in this species. In light of the high number of species that use rock crevices, however, Horned Puffins probably cohabit with several additional species. Several pairs of Common Murres on Ugaiushak Island nested in the larger, central area of a rock crevice, while a single pair of Horned Puffins nested in a small crevice or recess adjacent to this central area (Wehle, Chapter I).

The only reported instance of cohabitation in Rhinoceros Auklets was with Tufted Puffins (Frazer 1975). The apparent lack of cohabitation in this species may be attributed to habitat. The typically heavy vegetative cover may deter other species, particulary diurnal species susceptible to avian predation.

Considerable information is available on competition and cohabitation of nest-sites in Common Puffins. In a study of nest-site competition between Common Puffins and Manx Shearwaters, (Puffinus puffinus) Ashcroft (1976) found that competition for burrows appeared to be in balance between the two species, with the same proportion of puffin burrows becoming occupied by shearwaters as the proportion of shearwater burrows becoming occupied by puffins in successive years. Common Puffins had the competitive advantage in their optimal habitat, but shearwaters had the advantage in the remaining habitats. Some

cohabitation did occur, however, with roughly 10-20% of the burrows in puffin colonies being cohabited by the two species. In these cases, puffins occupied one tunnel within the burrow and shearwaters occupied another. Cohabitation of burrows by puffins and shearwaters has also been reported by Lockley (1953) and Dickinson (1958).

Other birds that cohabit with Common Puffins include Northern Fulmars (Fulmarus glacialis), Razorbills (Alca torda), and murres (Uria spp.) (Lockley 1953) and storm-petrels (Dickinson 1958). In most cases these species have nested either near the burrow entrance or in a side tunnel of the main burrow.

Finally, rabbits and puffins may interchange in the use of burrows (Lockley 1934, 1953; Ashcroft 1976;), and they even have been observed to cohabit the same burrow (Baxter and Rintoul 1953). In general, however, puffins will outcompete rabbits for burrows, so rabbits are not important competitors with puffins for nest-sites (Ashcroft 1976).

The species most frequently cohabiting with Tufted and Common Puffins are nocturnal (i.e., storm-petrels and Manx Shearwaters, respectively). Apparently, the temporal separation between the species at the time when nest-sites are selected promotes ecological segregation of nest-sites by reducing potential interspecific competition.

THE EGG STAGE

Egg-laying Dates

Timing of egg-laying in seabirds is chiefly determined by the accessibility of nest-sites and by the availability of food at a time when the female is forming the egg(s), and/or when the chick(s) are being fed (see "Arrival and Settlement").

The most important criteria determing the accessibility of nest-sites for puffins is the presence of ice, snow, and/or water over or in the nest-site (Belopol'skii 1957; Kozlova 1957; Uspenski 1958; Myrberget 1962; Sealy 1973b; Hornung and Harris 1976; Wehle, Chapter I). Generally, once these adverse conditions disappear, egg deposition follows almost immediately. These conditions probably impose their strongest influence on the timing of laying at the northern limits of the breeding ranges of Tufted, Horned, and Common puffins. Similarly, the influence of these conditions on the timing of laying of Rhinoceros Auklets is probably substantially less than for the other three puffins owing to the auklets' more southern distribution.

The onset of egg-laying in puffins generally occurs 2-5 weeks later at the northern than southern limits of their breeding ranges (Appendix I). Although various authors define "peak" egg-laying differently, usually one-half to two-thirds of a puffin population lay during a 1-3 week interval. The majority of the remaining population usually lay after rather than before this peak period. In areas of sympatry, peak egg-laying of Tufted Puffins generally coincides with

that of Rhinoceros Auklets but occurs approximately 1-2 weeks earlier than for Horned Puffins.

Intracolony variation in egg-laying has been attributed to several phenomena. Common Puffins breeding for the first time tend to lay later than experienced breeders (Ashcroft 1976). Tufted Puffins breeding in sub-optimal habitats tend to lay later than birds laying in preferred habitats (Frazer 1975). In Common Puffins, more birds breeding in the sub-optimal level habitat tend to lay earlier and later than do birds in the optimal slope habitat, with the result that laying is more synchronized on the slope habitat (Nettleship 1972). Furthermore, in successive years, egg-laying patterns for the first half of the laying period within each habitat are more similar on slope than on level habitat (Nettleship 1972). Similarly, Kartaschev (1960) reported differences of 15-20 days or more within a single season in the onset of egg-laying of birds on the same island, the variation being related to aspect of slope.

The interaction of varying climatic conditions with the onset and synchrony of egg-laying in Common Puffins has been summarized by Belopol'skii (1957): when climatic conditions are less favorable, the birds may lay early, but the length of the egg-laying period is considerably prolonged. In the extreme north, where the summer is short, egg-laying tends to be simultaneous.

There are conflicting reports on the relative timing of laying among pairs in the same colony in successive years. In eight pairs of Rhinoceros Auklets Leschner (1976) found the same rank order from one year to the next, and I (Wehle, Chapter I) found a similar pattern

in 9 of 12 pairs of Tufted Puffins. In Common Puffins, however, Ashcroft (1976) found no strong correlation between relative laying dates of pairs in successive years.

Egg Description

Egg color in all four puffin species is dull creamy-white with a tendency towards very pale bluish-white. Many eggs show a few, but some numerous, spots and/or scrawls of various shades of gray, blue, green, reddish-brown, and brown which tend to be concentrated in a wreath around the larger end. The location of pigments with the eggshell has been described by Bunyard (1922). Eggs of all four species tend to become soiled soon after laying and become dirty brown.

The significance of the patterns of coloration and markings exhibited in the eggs of puffins today remains a mystery. Several authors have suggested that puffin eggs are undergoing a de-pigmentation from a time when puffins may have nested in more open situations and had camoflaged eggs (Whatmough 1949, Kaftanovskii 1951, Lack 1953, and others). These authors reasoned that with enclosed nests, pigmentation was no longer advantageous and may even have been selected against, since light eggs are easier for birds to locate in dim light. In contrast, Bunyard (1922) contended that Common Puffin eggs were passing through a rapid transition state in that the pigment was becoming more super-imposed. Bunyard failed, however, to identify any selective force favoring the increased pigmentation.

Tufted Puffin eggs are significantly larger and heavier than Horned Puffin eggs (Wehle, Chapter I and Table 42). Horned Puffin and Rhinoceros Auklet eggs tend to overlap in size, though the latter are slightly larger on the average (Table 42). Common Puffin eggs are the smallest of any of the puffin species (Table 42). Proportionate egg weight (egg weight ÷ adult body weight) in puffins ranges from 9.5% to 15.5% (Table 42). Common Puffins tend to lose a greater proportion of their egg weight during incubation than do either Tufted or Horned puffins (Table 43), presumably because of their smaller size.

Egg Replacement

All four species of puffins generally lay one egg per breeding season. Two eggs in one nest, however, has been reported for Tufted Puffins (Dement'ev and Gladkov 1951, Frazer 1975), Horned Puffins (Dement'ev and Gladkov 1951, Kozlova 1957), and Common Puffins (Bent 1919, Witherby et al. 1941, Whatmough 1949, Dement'ev and Gladkov 1951, Kozlova 1957, Kartashev 1960, Myrberget 1962, Lockley 1953), although it is not known for sure whether the second eggs in these situations were laid by the same bird. It is significant that puffins develop two lateral brood patches. The possession of two brood patches in species which lay only a single egg has been discussed by Fisher and Lockley (1954), Wynne-Edwards (1955, 1962), Lack (1954), and others. These authors suggest that at some point in their evolutionary past, these alcids laid two eggs but in modern times

Table 42. Fresh egg weight, adult body weight, and proportion of egg weight to adult body weight in puffins.

Location	Fresh Egg Weight (g) N	Mean	Range		Adult Body Weight (g) N	Mean	Range	Proportionate Egg Weight (%)	Source
Tufted Puffin									
Buldir Island, AK	37	94.4	81.0-107.5		79	755	643-862	12.5	Wehle (Chapter I)
Ugalushak Island, AK	80	94.3	81.0-110.0		34	792	986-740	11.9	Wehle (Chapter I)
Barren Islands, AK	32	92.8	84.0-107.0		33	784	700-870	11.8	Amaral (1977)
various	?	91.0			11	797	689-920	11.4	Schonwetter (1963) (egg wt.) Sealy and Bedard (1973) (body wt.)
Horned Puffin									
Buldir Island, AK	19	76.2	68.5-86.5		64	491	415-602	15.5	Wehle (Chapter I)
Ugalushak Island, AK	53	75.1	63-84		21	526	445-594	14.3	Wehle (Chapter I)
Barren Islands, AK	3	74.0	73.5-76.0		1	607		12.3	Amaral (1977)
St. Lawrence Island, AK	2	57.1	56.1-58.1		22	599	499-574	9.5	Sealy (1973)
Rhinoceros Auklet									
Protection Island, WA	15	77.7	68-88		51	521		14.9	Wilson (1977) (egg wt.) Leschner (1976) (body wt.)
various	?	77.0			10	518		14.7	Schonwetter (1974) (egg wt.) Summers (1970) (body wt.)
Common Puffin									
Great Island, Newfoundland (slope)	90	65.5		(m)	18	491.6	432-524	13.3	Nettleship (1972)
				(f)	29	439.9	386-511	14.9	Nettleship (1972)
(level)	60	65.1		(m)	21	468.3	429-513	13.9	Nettleship (1972)
				(f)	28	451.4	402-498	14.4	Nettleship (1972)
Cape Whittle, Gulf of St. Lawrence	30	55.9	54.5-73.2		29	476	407-542	11.7	Johnson (1944)
Skomer Island, U.K.	28	59.2	53-65		158	385	310-488	15	Corkhill (1972)
USSR	?	65.0	50-71					13	Kartashev (1960)

Table 43. Percent of egg weight loss during incubation for Tufted, Horned, and Common puffins.

Species	N	Percent egg weight loss Mean	Max.	Min.	Source
Tufted Puffin	5	17	22	13	Manuwal and Boersma (1978)[a]
	9	13.2	14.8	10.9	Wehle (Chapter I)
Horned Puffin	5	12.1	13.8	8.9	Wehle (Chapter I)
Common Puffin	?	16.5			Belopol'skii (1957)
	1	21.7			Corkhill (1972)
	?	c. 33			Ashcroft (1976)

[a]Eggs incubated by bantam hen.

lay only one egg in response to long-term environmental changes and/or changes in population size and structure. With this probable evolutionary history, it is not surprising that an occasional bird may lay a two-egg clutch.

Most puffins apparently lay a replacement egg if the first egg is deserted or lost. In an experimental removal of first clutches from Tufted and Horned puffin nests, 70% and 30%, respectively, contained replacement clutches (Wehle, Chapter I). Replacement laying in Rhinoceros Auklets has been suggested by Richardson (1961) and Leschner (1976), although there are no data on its frequency. Replacement laying in Common Puffins has been reported by Perry (1940), Dement'ev and Gladkov (1951), Belopol'skii (1977), Uspenski (1958), Kartashev (1960), Myrberget (1962), Nettleship (1972), Ashcroft (1976), and M. P. Harris (pers. comm.). Of 17 nests observed, Belopol'skii (1957) found four (24%) contained a second clutch and one (6%) contained a third clutch. Egg replacement time for each of the four puffin species ranges from 1.5 to 3 weeks (Table 44).

The amount of time and the amount of food required for the production of a second clutch is determined by the size of the egg(s) in relation to adult body weight (Lack 1968). The length of time between the laying of the first and second clutches is also dependent on the availability and proximity of food to the breeding colony.

In most areas where puffins breed, deteriorating environmental conditions late in the breeding season also probably impose a time limit on successful replacement laying. In a year when laying was late, Ashcroft (1976) found that all replacement layings by Common Puffins

Table 44. Egg replacement time (the interval from the loss or desertion of the first egg to the appearance of the second egg) for puffins.

Species	Replacement Time (Days)	Source
Tufted Puffin	10-21	Wehle (Chapter I)
Horned Puffin	16-20	Wehle (Chapter I)
Rhinoceros Auklet	9-22	Leschner (1976)
Common Puffin	10(?)-17	Uspenski (1958), Kartashev (1960), Ashcroft (1976)

were made in the first third of the laying period.

As a result of these factors, selection has apparently favored replacement laying in the puffins. It is likely, however, that local conditions, especially proximity to sufficient food resources, exert a strong influence on whether puffins will lay replacement clutches in any particular colony or year.

Incubation Rhythm

Incubation in all puffin species is shared by both sexes (Dement'ev and Gladkov 1951, Lockley 1953, Belopol'skii 1957, Kozlova 1957, Uspenski 1958, Richardson 1961, Kartashev 1960, Myrberget 1962, Amaral 1977, and others). In general, the sexes exchange incubation duties at least once daily (Heath 1915; Willett 1915; Kozlova 1957; Richardson 1961: Myrberget 1962; Amaral 1977; Summers and Drent 1979; Wehle, Chapter I), but single shifts have been reported of over 1 day in Tufted Puffins (Amaral 1977) and Horned Puffins (Wehle, Chapter I), 4 days in Rhinoceros Auklets (Wilson 1977), and 3-4 days in Common Puffins (Myrberget 1962). The incubation rhythm of Tufted Puffins may be flexible. Based on activity cycle data, I estimated a 4-5 day incubation shift for this species on Buldir Island (Wehle 1976). Longer than normal incubation shifts may be the result of patchy food distribution close to the colony and/or of birds having to travel considerable distances to feed (Ashmole and Ashmole 1967, Lack 1968, Ashmole 1971, Sealy 1976).

During the day, Tufted, Horned and Common puffins regularly leave their egg unattended for several hours, during which time both adults generally loaf outside of the burrow (Lockley 1953, 1954; Kartashev 1960; Amaral 1977; Wehle, Chapter I). Also, Tufted and Horned puffins and Rhinoceros Auklets may temporarily desert their eggs for several days (Amaral 1977; Wilson 1977; Summers and Drent 1979; Wehle, Chapter I). In most cases eggs which were temporarily deserted subsequently hatched, attesting to their ability to withstand considerable chilling. Lack (1968) suggests that the resistence of an embryo to chilling may be an adaptation in offshore feeders, whose food supply is patchily distributed and, as a result, the incubating parent leaves the nest prior to the return of its mate.

Length of Incubation

The mean lengths of incubation for Tufted Puffins and Rhinoceros Auklets are several days longer than for Horned and Common puffins (Table 45). Also, Tufted Puffins and Rhinoceros Auklets both exhibit a greater degree of variability in their length of incubation than the other two species. This variability may be the result of a number of factors, including irregular brooding during the first several days (Dement'ev and Gladkov 1951; Kozlova 1957; Kartashev 1957; Myrberget 1962; Wilson 1977; Wehle, Chapter I), temporary desertion of the egg for one to several days during incubation (see "Incubation Rhythms"), and variation in the length of the hatching period (Table 46).

Table 45. Length of incubation (days) in puffins.

	N	Mean	Range	Source
Tufted Puffin				
		c. 45		Sealy (1973)
			38-48	Frazer (1975)
	11	45.2	43±2.5-53±2.5	Amaral (1977)
		46.5	42.5±1.0-53±1.0	Wehle (Chapter I)
Horned Puffin				
	5	41.4	40-43	Sealy (1969)
	5	40.2	39±2.0-42±2.0	Amaral (1977)
Rhinoceros Auklet				
	10	45.5	42-49	Leschner (1976)
	28	44.9	39-52	Wilson (1977)
		42		Summers and Drent (1979)
Common Puffin				
		35		Dement'ev and Gladkov (1951)
		41.5	40-43	Lockley (1953)
			35-36	Belopol'skii (1957)
		35		Kozlova (1957)
			35-42	Kartashev (1960)
		41.8	40-45	Myrberget (1962)
		39	36-43	Ashcroft (1976)

Table 46. Length of the hatching period (days) in puffins.

	N	Mean	Range	Source
Tufted Puffin	7	3.3	2-6	Wehle (Chapter I)
	16	4.3	1-12	Wehle (Chapter I)
Horned Puffin	2	4.5	4-5	Sealy (1970)
	2	3.0	2-4	Wehle (Chapter I)
Rhinoceros Auklet	4		1	Wilson (1977)
Common Puffin			2-3	Kartashev (1960)
	13	4.3	3-5	Myrberget (1962)

Among the alcids, puffins have the longest incubation periods with respect to both proportionate and absolute egg size (Sealy 1972). The two species of puffins having the largest eggs (Tufted Puffins and Rhinoceros Auklets) have slightly longer incubation periods than the smaller-egged Horned and Common puffins. In seabirds, the length of incubation is strongly correlated with the length of the nestling period (Lack 1968). Lack contended that this relationship developed because the easiest way to evolve a slower rate of growth for the nestlings is to retard the growth process as a whole, including that of the embryo. Further, he points out that slow growth is advantageous for species with sparse food supplies. This relationship is supported by the puffins, in that the two species having the longest incubation periods are also the two species which generally feed farthest from shore (see "Feeding of Adults").

THE NESTLING STAGE

Hatching

Young puffins hatch with the aid of a single egg tooth located near the tip of the upper mandible. Other alcids (Uria, Cepphus, Synthliboramphus, Endomychura, and Brachyramphus) also have egg teeth or teeth-like structures on their lower mandibles (Sealy 1970).

In Tufted and Horned puffins, as in most other alcids, the egg tooth gradually disappears over the course of several weeks after hatching. However, if subjected to unusually rough treatment, the

egg tooth may fall off earlier. In 27 Tufted Puffin chicks studied, 13 (48%) lost their egg tooth between 2 and 3 weeks after hatching, and 3 chicks still retained their egg tooth when 4 weeks old (Wehle, Chapter I). Of 28 Horned Puffin chicks, 16 (57%) lost their egg tooth 1-2 weeks after hatching and all chicks had lost it by 4 weeks of age (Wehle, Chapter I).

The egg tooth of Rhinoceros Auklets is deciduous (Sealy 1970). In 20 Rhinoceros Auklet chicks studied by Wilson (1977), the mean retention time of the egg tooth was 4.4 days with a range of 2-8 days. The retention time of egg teeth in Common Puffins has not been reported.

Adults of all puffin species typically remove the eggshell from the nest within a couple of days after the chick hatches. In most cases, the eggshell is left at or near the entrance to the nest-site. In gulls (Laridae), removal of the eggshells from the nest-site is considered a naturally selected device to prevent advertising the nest-site to predators (Welty 1975). Apparently the potential danger to puffin chicks as a result of leaving their shells in a conspicuous location outside of the nest-site is offset by the nest-site's relative inaccessibility to predators.

Brooding Period

There is considerable interspecific and intraspecific variation in the length of time adult puffins brood their chicks after hatching (Table 47). Rhinoceros Auklets tend to brood their chicks for the

Table 47. Age (days) at which puffin brooding is terminated.

	Mean	Range	Source
Tufted Puffin		3-5	Cody (1973)
		0-4	Amaral (1977); Manuwal and Boersma (1978)
		0-3	Wehle (Chapter I)
Horned Puffin	6.4	4-9	Amaral (1977); Manuwal and Boersma (1978)
		5-7	Wehle (Chapter I)
Rhinoceros Auklet	Little or no brooding		Richardson (1961)
		1-3	Leschner (1976)
	3.9	0-9	Wilson (1977)
	2		Summers and Drent (1979)
Common Puffin	c. 7		Rol'nick (1948)
		6-7	Dement'ev and Gladkov (1951)
	c. 7		Ashcroft (1976)

shortest time followed in decreasing order of brooding length by Tufted, Horned, and Common puffins.

There does not appear to be any correlation between the length of the brooding period and adult body size or the type of nest-site typically used. However, brooding is shortest in the two species (Rhinoceros Auklets and Tufted Puffins) which typically feed farthest from shore (see "Feeding of Adults"). Also, intraspecific variation in brooding may reflect the relative foraging efficiencies of the adults (Harris 1969).

Length of the Nestling Period

The nestling period is defined as the interval from the total emergence of the chick from the shell to the permanent departure of the chick from the nest-site. Puffins have a semi-precocial post-hatching development pattern in which the young are fed in the nest until they are at least two-thirds of adult-size and in complete juvenal plumage (Sealy 1973a). Some puffin chicks leave their nest-sites, especially at night, and wander around the colony for short periods of time prior to fledging. However, once the birds leave the breeding colony, they do not return to their nest-site.

Puffins have the longest nestling periods of any alcids (Sealy 1972). Prolonged nestling periods among semi-precocial alcids are correlated with slower growth rates of young, which apparently have evolved to reduce their energy requirements per unit time (Sealy 1973a). This interspecific variation in growth rate, in turn, is related to the feeding capacities of the adults (Sealy 1973a).

The length of the nestling period is generally longer for Tufted Puffins and Rhinoceros Auklets than for Horned and Common puffins (Table 48). These differences probably reflect the entire spectrum of factors associated with feeding young including food availability and abundance, feeding rate, foraging efficiency, weather conditions, experience of adults, etc.

BREEDING SUCCESS

The breeding success of puffins may be compared in terms of four components of success: 1) laying success, the percent of nest-sites studied which contained eggs, 2) hatching success, the percent of eggs which hatched, 3) fledging success, the percent of chicks hatched which survived to fledging, and 4) total breeding success, the percent of eggs laid which gave rise to fledglings. Tables 49-52 present the available information on breeding success of puffins in terms of these components; in some cases, rates have been calculated from data provided in the literature. Available data beyond these rates are included under self-explanatory headings in the tables.

In most colonies, and between years at the same colony, laying success of Tufted Puffins has been approximately 50-60% (Table 49). For the two years in which laying success was determined for Rhinoceros Auklets, success rates were slightly higher than for Tufted Puffins. Although there are no specific data on laying success of Common Puffins, a proportion of pairs on the colonies occupy nest-sites but do not lay (Ashcroft 1976; M. P. Harris, pers. comm.).

Table 48. Length of the nestling period (days) in puffins.

	N	Mean	Range	Source
Tufted Puffin	?	55		Cody (1973)
	1	51		Frazer (1975)
	9	47	44-48	Amaral (1977)
			55-59	Leschner and Burrell (1977)
	4		44-48	Moe and Day (1979)
	3		39-49	P. A. Baird and R. A. Moe (pers. comm.)
	9	50.4	43-59	G. Burrell (pers. comm.)
	6		38-41	R. Gill (pers. comm.)
	1	47		Vermeer et al. (1979)
	9	44.8	40-48	Wehle (Chapter I)
	4	41.8	41-42	Wehle (Chapter I)
Horned Puffin	1	39±3		Swartz (1966)
	1	38		Sealy (1969)
		40	38-42	Amaral (1977)
	1		39	Leschner and Burrell (1977)
	1		43	Wehle (Chapter I)
	1		34	Wehle (Chapter I)
Rhinoceros Auklet			35-42	Richardson (1961)
		56		Cody (1973)
	19	54.3	50-60	Leschner (1976)
	37	51	42-62	Leschner (1976)

Table 48. Continued

	N	Mean	Range	Source
			56	DeGange et al. (1977)
	4		45-54	Leschner and Burrell (1977)
	12	50	38-56	Summers and Drent (1979)
		48.3	42-57	Manuwal (unpubl. data)
		49.3	42-56	Wilson (unpubl. data)
Common Puffin	3		49-52	Lockley (1934)
			36-40	Dement'ev and Gladkov (1951)
		42		Belopol'skii (1951)
			39-46	Kozlova (1957)
			36-37	Uspenski (1958)
			35-46	Uspenski (1958)
			38-45	Kartashev (1960)
		47.7	43-52	Myrberget (1962)
		38	34-51	Pearson (1968)
		37.3		Corkhill (1972)
		54.5	39-83	Nettleship (1972)
		38	34-44	Ashcroft (1976)
	37	41.2		Harris (1978)
	65	39.6		Harris (1978)

Table 49. Breeding success of Tufted Puffins.

	Destruction Island, WA 1975	Triangle Island, B.C. 1975	Triangle Island, B.C. 1976	Triangle Island, B.C. 1977	Buldir Island, AK 1975	Hall Island, AK 1976	Chowiet Island, AK 1976
Total no. of burrows					54		
No. burrows with eggs	11	77	70	111	26	51	38
Laying success					48%		
No. eggs hatched	11	62	3	59	5	32	16
Hatching success	100%	80.5%	4.3%	53.2%	19%	62.7%	42%
Egg mortality	0%	19.5%	95.7%	46.8%	81%	37.3%	58%
Percent of total burrows to hatch eggs					9%		
No. chicks monitored					2		
No. of chicks fledged	11	35	1	1	2		9
Percent of total burrows to fledge chicks							
Fledging success	100%	56.5%	33.3%	1.9%	0-100%		56%
Chick Mortality	0%	43.5%	66.7%	98.1%	0-100%	16.7%	44%
Total breeding success		45.5%	1.4%	0.9%		52.4%	24%
Source	(1)	(2)	(2)	(2)	(3)	(4)	(5)

Table 49. Continued

	Ugaiushak Island, AK 1976	Ugaiushak Island, AK 1977	Sitkalidak Island, AK 1977	Nelson Islands, AK 1977	Barren Islands, AK 1977	Barren Islands, AK 1977	Cliff Island, AK 1977
Total no. of burrows	94	167	93		85	100	
No. burrows with eggs	52	99	67		40	56	25
Laying success	55%	59%	76%		47%	56%	
N. eggs hatched	31	82		7	16	28	22
Hatching success	60%	83%	61%		40%	50%	88.6%
Egg mortality	40%	17%	39%		60%	50%	12%
Percent of total burrows to hatch eggs	33%	49%			19%	28%	
No. chicks monitored	50	21					
No. of chicks fledged	43	20		6	11	22	20
Percent of total burrows to fledge chicks					13%	22%	
Fledging success	80-86%	62-95%	88%	85.7%	69%	79%	90.0%
Chick Mortality	14-20%	5-38%	12%	14.3%	31%	21%	9.1%
Total breeding success					28%	39%	80%
Source	(3)	(3)	(6)	(7)	(8)	(9)	(10)

sources: (1) G. Burrell, pers. comm., (2) Vermeer et al. 1979, (3) Wehle, Chapter I, (4) Moe and Day 1979, (5) Leschner and Burrell 1977, (6) Baird and Moe 1978, (7) R. Gill, pers. comm., (8) Amaral 1977, (9) Manuwal and Boersma 1978, (10) Nysewander and Hoberg 1978.

Table 50. Breeding success of Horned Puffins.

	Buldir Island, AK 1975	Big Koniuju Island, AK 1976	Hall Island, AK 1976	Chowiet Island, AK 1976	Ugaiushak Island, AK 1977
No. nests with eggs		20	12	48	68
No. eggs hatched		16	10	32	52
Hatching success		80%	83.3%	66.6%	76%
Egg mortality		20.0%	16.6%	33.4%	24%
No. chicks monitored	2				11
No. chicks fledged	2			19	10
Fledging success	0-100%	72.0%	83.4%	59.4%	9-91%
Chick mortality	0-100%	28.0%	16.6%	40.6%	9-91%
Total breeding success				39.6%	
Source	(1)	(2)	(2)	(3)	(1)

Table 50. Continued

	Barren Islands, AK 1976	Barren Islands, AK 1977	St. Paul Island, AK 1975	St. Paul Island, AK 1976	St. Paul Island, AK 1977
No. nests with eggs	14	14	11	25	10
No. eggs hatched	11	13	11	14	9
Hatching success	79%	93%	100%	56%	90%
Egg mortality	21%	7%	0%	44%	10%
No. chicks monitored					
No. chicks fledged	4	9	5-11	11	7-8
Fledging success	36%	69%	45-100%	79%	78-79%
Chick mortality	64%	31%	0-55%	21%	11-22%
Total breeding success	29%	64%	45-100%	44%	70-78%
Source	(4)	(5)	(6)	(6)	(6)

source: (1) Wehle, Chapter I, (2) Moe and Day 1979, (3) Leschner and Burrell 1977, (4) Amaral 1977, (5) Manuwal and Boersma 1978, (6) Hunt et al. 1978.

Table 51. Breeding success of Rhinoceros Auklets.

	Destruction Island, WA 1974	Destruction Island, WA 1975	Protection Island, WA 1975	Protection Island, WA 1976	Cleland Island, B.C. 1969	Triangle Island, B.C. 1976	Forrester Island, AK 1976	Chowiet Island, AK 1976
Total no. of burrows	64	84	82	80		68		
No. of burrows with eggs					49			45
Laying success			65.0%	62.1%				
No. eggs hatched	19	37			44			32
Hatching success			81.5%[a]	91.1%[a]	90%		77%	71.1%
Egg mortality					10%		23%	28.9%
Percent of total burrows to hatch eggs	29.7%	44.0%	33.8%	39.0%				
No. chicks monitored					18			
No. chicks fledged	15	31			13			23
Percent of burrows to fledge chicks	23.4%	36.9%				59%		
Fledging success	78.9%	83.8%	92.6%	96.9%	72%			71.9%
Chick mortality	21.1%	16.2%	7.4%	3.1%	28%		29%	28.1%
Total breeding success					66%		48%	51.1%
Source	(1)	(1)	(2)	(2)	(3)	(4)	(5)	(6)

[a]Burrows not disturbed during incubation.

sources: (1) Leschner 1976, (2) Wilson 1977, (3) Summers and Drent 1979, (4) Vermeer et al. 1979, (5) DeGange et al. 1977, (6) Leschner and Burrell 1977.

Table 52. Breeding success of Common Puffins

	Great Island, Canada (slope) 1968	Great Island, Canada (slope) 1969	Great Island, Canada (level) 1968	Great Island, Canada (level) 1969	Funk Island & Small Island, Canada 1969	Skokholm, U.K. 1955-1958
Total no. of burrows						
No. burrows with eggs	90	200	60	202	253	697
No. eggs hatched	58	151	28	110		
Hatching success	64.4%	75.5%	46.6%	54.4%		
Egg mortality	35.6%	24.5%	33.4%	45.6%		
No. chicks fledged	25	101	6	48		229
Fledging success	43.2%	66.9%	21.4%	43.6%		98%
Chick mortality	56.8%	33.1%	78.6%	56.4%		2%
Chicks fledged/from undisturbed burrows						
Chicks fledged/burrows						
Chicks fledged/egg						
Total breeding success	27.7%	50.5%	10.0%	23.8%	90.5%	
Source	(1)	(1)	(1)	(1)	(1)	(2)

Table 52. Continued

	Skomer Island, U.K. 1973	Skomer Island, U.K. 1974	Skomer Island, U.K. 1975	Lovunden, Norway 1955
Total no. of burrows	54	129	87	
No. burrows with eggs				
No. eggs hatched				63
Hatching success	49%	78%	76%	
Egg mortality	51%	22%	24%	
No. chicks fledged				57
Fledging success	93.1%	94.0%	96.5%	90.8%
Chick mortality	6.9%	6.0%	3.5%	9.2%
Chicks fledged/from undisturbed burrows	0.66	0.605	0.66	
Chicks fledged/burrow	0.41	0.615	0.67	
Chicks fledged/egg	0.44	0.73	0.73	
Total breeding success				
Source	(3)	(3)	(3)	(4)

sources: (1) Nettleship 1972, (2) Dickinson 1958, (3) Ashcroft 1976, (4) Myrberget 1962.

Laying success of Horned Puffins has not been determined because of the difficulty of locating nest-sites prior to egg deposition. Thus, in at least three species, a proportion of the puffins present on the breeding colonies each year occupy nest-sites but do not lay. Three possible explanations for this are 1) the birds are reproductively immature and are "prospecting," 2) the female is in too poor condition to lay, and 3) selection has acted to defer laying in birds which could not secure nest-sites, as a result of competition or interference with other birds, early enough in breeding season to allow chick fledging.

The first explanation would seem the most likely, as roughly the same proportion of nest-sites are occupied by non-breeders in different colonies, in different years at the same colony, and in different species. However, at least a portion of non-breeders occupying nest-sites are adult birds, and some are pairs known to have bred in previous years (Ashcroft 1976, M. P. Harris, pers. comm.).

Although food-related factors have been attributed to the failure of albatrosses (Diomedeidae) and Royal Penguins (Eudyptes schlegeli) to lay (Fisher 1967, Carrick and Ingham 1967, respectively), the inability of female puffins to acquire sufficient energy reserves for egg formation would not account for the approximately equal proportion of non-breeders observed under such a wide variety of conditions.

The third explanation would be most likely to occur in colonies when competition for nest-sites is keen, i.e., when nest-sites are limiting or nearly so. There is no evidence to suggest significant competition in the Rhinoceros Auklet colony or in any of the Tufted

Puffin colonies in which laying success was measured. This, in conjunction with the fact that birds occupied nest-sites but did not lay, indicates that these non-breeding puffins are not members of a true "floater" population (Brown 1969). Hence, at this time, there is no acceptable explanation to account for the varying proportions of puffin populations which occupy nest-sites but do not breed.

Hatching success in my studies appeared to increase significantly each year; however, this increase probably reflected lower desertion rates with improved monitoring techniques rather than actual biological variation. Similar progressively higher success rates are evident in the studies of other investigators. It is difficult to distinguish natural desertion from that caused by human disturbance, and most values of hatching success presented in Tables 49-52 are probably lower than they would have been under natural conditions. This possible discrepancy is probably least true for Horned Puffins, whose nest-sites frequently allow for observation of contents with minimum disturbance. In general, hatching success of all puffin species under natural conditions is probably 75-90%.

For a variety of reasons, other than human disturbance, some puffins desert their eggs prior to hatching. In Tufted Puffins, the natural desertion rate is probably 5-15% (Manuwal and Boersma 1978; Wehle, Chapter I). Similarly, in two undisturbed sample plots of Rhinoceros Auklets, 14% and 9-19% of the eggs were deserted (Leschner and Burrell 1977; Wilson 1977, respectively).

The main causes of egg mortality in puffins are 1) desertion or loss from disturbance by other birds or animals (Ashcroft 1976; Wilson

1977; Wehle, Chapter I), 2) desertion or inviability related to weather (Perry 1940; Nettleship 1972; Hornung and Harris 1976; Wilson 1977; Wehle, Chapter I), 3) infertility (Nettleship 1972; Amaral 1977; Summers and Drent 1979; Wehle, Chapter I), and 4) predation (Perry 1940; Myrberget 1962; Nettleship 1972; Birkhead 1974; Cramp et al. 1974; Ashcroft 1976; Wehle, Chapter I).

For all colony-years presented in Tables 47-50, the average fledging success is approximately 60-70% for Tufted Puffins, 53-77% for Horned Puffins, 82% for Rhinoceros Auklets, and 72% for Common Puffins. Much of the intraspecific variation in fledging success among colonies and among years at the same colony is correlated with weather (Nettleship 1972, Amaral 1977), food availability (Vermeer et al. 1979, Wehle, Chapter I), and predation or cleptoparasitism (Nettleship 1972). The influence of weather and food availability on fledging success within a specific colony appears more variable between years than does predation, which is probably more consistent from one year to another.

Species reported preying on puffin nestlings include River Otters (Lutra candensis), Arctic Foxes (Alopex lagopus), Arctic Ground Squirrel, (Spermophilus undulatus), rats, (Rattus spp.) cats (Felis domesticus), Great Skuas, (Stercorarius skua), Common Ravens, (Corvus corax), crows (C. spp.), and gulls (Larus spp.) (Perry 1940; Lockley 1953; Myrberget 1962; Nettleship 1972; Cramp et al. 1974; Ashcroft 1976; Leschner 1976; Leschner and Burrell 1978; Wehle, Chapter I).

Other factors contributing to chick mortality of puffins include crushing of burrows by other animals (Willett 1912), parasite infestation

(Lockley 1953), eye infection (Myrberget 1962, Ashcroft 1976), peck wounds inflicted by adults or other birds (Leschner and Burrell 1979), interference from other birds (Wilson 1977), and choking on food (Summers and Drent 1979).

Most puffin chick mortality occurs within the first 2 weeks after hatching (Myrberget 1962; Nettleship 1972; Ashcroft 1976; Wilson 1977; Wehle, Chapter I). Older chicks are less likely to die; they chill less easily and are more mobile, and can seek refuge from predators and flooding. Later mortality is probably due primarily to starvation.

Values of total breeding success in puffins has varied from 0.9% (Vermeer et al. 1979) to 90.5% (Nettleship 1972) (Tables 49-52). Variation in total breeding success is affected in part by the variety of factors previously mentioned, with the single most important factor probably being food availability.

In addition, several other variables affect total breeding success. Nettleship (1972) and Ashcroft (1976) reported that Common Puffins which laid earlier were more likely to successfully raise a chick than those which laid later. Several explanations may account for this phenomenon (Ashcroft 1976): 1) late layers tend to be inexperienced breeders, birds in poorer condition, or less efficient feeders; 2) birds laying later may suffer greater disturbance from other birds, and 3) chicks which hatch later may suffer a higher mortality from progressively inclement weather in the later part of the breeding cycle. Also, the abundance and availability of food resources are most favorable to birds which lay early.

The location of nest-sites within the colony may sometimes affect breeding success. In Newfoundland, Common Puffins nesting in slope habitat had a higher total breeding success than did birds nesting in level habitat (Nettleship 1972), because of lower gull predation and cleptoparasitism. On the other hand, in Great Britain Ashcroft (1976) found that position of Common Puffin nest-sites did not affect productivity, nor did burrow length or depth.

Finally, the probability of an individual pair breeding successfully in future years is positively correlated with their breeding success in previous years. Ashcroft (1976) found that Common Puffins which bred successfully in one year were more likely to breed successfully in subsequent years, while pairs which failed in one year were also more likely to fail in subsequent years.

PREDATION AND CLEPTOPARASITISM OF ADULT PUFFINS

At least 13 species of birds and 5 species of mammals have been reported to prey on the four puffin species (Table 53). Mortality of adult puffins by predation is probably minimal in most colonies, although in a few locations, adult puffins may comprise a considerable proportion of the diet of certain predators (e.g., Bald Eagle [Wehle, Chapter I] and Arctic Fox [J. L. Trapp, pers. comm.]).

Virtually all of the information of predation of puffins pertains to avian or mammalian predators at breeding colonies. However, some alcids have been recorded in the stomachs of predatory fish (Preble and McAtee 1923, Bigelow and Welsh 1924, Tuck 1961), and it seems likely that puffins may also be killed by marine fish.

Table 53. Predators (p) and cleptoparasites (c) of adult puffins.

	Tufted Puffin (a) (b) p c	Horned Puffin (c) (d) p c	Rhinoceros Auklet (e) (f) p c	Common Puffin (g) (h) p c	Source
Goshawk (Accipiter gentilis)				x	(g) 24
Grey Sea Eagle (Haliaetus leucoryphus)				x	(g) 24
Bald Eagle (H. leucocephalus)	x	x	x		(a) 2, 16, 37 (c) 2, 37 (e) 16
Gyrofalcon (Falco rusticulus)				x	(g) 24
Peregrine Falcon (F. peregrinus	x	x		x	(a) 2, 37 (c) 2, 37 (g) 25, 29
Great Skua (Stercorarius skua)				x	(g) 3, 14
Parasitic Jaeger (S. parasiticus)	x	x		x	(b) 37 (d) 37 (h) 3, 4, 5, 8, 21, 23, 24
Glaucous-winged Gull (Larus glaucescens)	x	x x			(b) 12, 26, 37 (c) 11 (d) 35
Great Black-backed Gull (L. marinus)				x x	(g) 6, 7, 14, 17, 18, 25, 29, 31 (h) 18, 28
Lesser Black-backed Gull (L. fuscus)				x	(h) 5, 6, 13
Western Gull (L. occidentalis)			x?		(e) 32
Herring Gull (L. argentatus)				x x	(g) 29 (h) 5, 6, 13, 14, 18, 27, 28
Mew Gull (L. canus)				x	(h) 14
Unidentified Gull (Larus sp.)	x		x	x	(b) 19 (f) 30 (h) 23, 33
Great Horned Owl (Bubo virginianus)			x		(e) 30, 35
Snowy Owl (Nyctea scandiaca)	x	x		x	(a) 36, 37 (c) 37 (g) 24
Jackdaw (Corvus monedula)				x	(h) 6, 10, 13, 27
Common Raven (C. corax)				x	(g) 25
Arctic Fox (Alopex lagopus)	x	x			(a) 15, 34 (c) 15
Red Fox (Vulpes fulva)	x?	x?			(a) 15 (c) 15
Unidentified Fox				x	(g) 22
Mink (Mustela nigon)				x	(g) 22
River Otter (Lutra candensis)	x				(a) 2
Cat or Dog (Felis domesticus or Canis familiaris)			x		(e) 1, 35
Marine Gosefish (Lophius americanus)				x?	(g) 9

sources: (1) Alw 1967; (2) Amaral 1977; (3) Anderason 1976; (4) Arnason 1978; (5) Arnason and Grant 1978; (6) Ashcroft 1976; (7) Beason 1970; (8) Belopol'skii 1957; (9) Bluchow and Walsh 1924; (10) Birkhead 1974; (11) G. V. Byrd, pers. comm.; (12) Cody 1973; (13) Corkhill 1973; (14) Cramp et al. 1974; (15) H. H. Day, pers. comm.; (16) Delianys and Nelson 1978; (17) Dickinson 1958; (18) Evans 1975; (19) Frazer 1975; (20) Gordon 1941; (21) Grant 1971; (22) Grant and Nettleship 1971; (23) Harris 1978; (24) Kartashev 1960; (25) Lockley 1934; (26) Manuwal and Boersma 1978; (27) Myhre 1968; (28) Nettleship 1972; (29) Perry 1940; (30) Richardson 1961; (31) Saunders 1973; (32) Scott et al. 1974; (33) Skokova 1974; (34) J. L. Trapp, pers. comm.; (35) Wilson 1977; (36) Williams and Frank 1979 (37) Wehle, Chapter 1.

Cleptoparasitism of puffins, the robbery or piracy of food being carried by puffins to their nestlings, may significantly lower the fledging success of puffins in some colonies (Grant 1972, Nettleship 1972, Andersson 1976, Arnason 1978, Arnason and Grant 1978). At least 8 species of birds have been reported as cleptoparasites of puffins (Table 53). Cleptoparasitism appears to be much more common in colonies of Common Puffins than in those of the three Pacific puffins.

FEEDING OF ADULTS

Puffins capture their prey by pursuit diving (Ashmole 1971), using their partially opened wings for propulsion. Structural and physiological adaptations to this feeding technique and to the types of prey taken include 1) a marked increase in compactness and strength of the skeleton and in a reduction of the wing for increased efficiency in underwater "flight" (Storer 1945, 1960; Kuroda 1954, 1955a, 1967), 2) modification of the tongue and bill (Bedard 1969), and 3) ability to increase specific body weight and decrease heart rate while diving (Dement'ev and Gladkov 1951, Welty 1975).

In general, puffins feed singly but may also feed in monospecific or mixed species assemblages (Sealy 1973c; Ashcroft 1976; Wehle, Chapter I). Possible intraspecific cooperation in feeding among Common Puffins has been suggested by Ashcroft (1976). She found that, during the nestling period, birds from the same area of the colony tended to leave, feed, and return to the colony in groups of 2-5. These groups sometimes tended to provide their chicks with a more

similar amount of food on any given day than did puffins from all areas. From this evidence, she suggested that puffins may cooperate in finding the location of a good feeding area or that they could arrive at a feeding area together and benefit from fishing as a group, or both. There was, however, no evidence to indicate that birds feeding in small groups were more successful than birds feeding singly. I have observed similar small-group activity during the nestling period in Tufted Puffins and Horned Puffins.

There is currently no reliable information on the depths at which puffins feed; however, most prey are probably taken within 15 m of the surface (Harris and Hislop 1978; Wehle, Chapter I).

The distances puffins travel to feed from their breeding colonies may be compared in terms of three basic foraging habitats (see "Feeding of Adults," Chapter I): inshore waters, offshore waters, and oceanic waters. For the purposes of the following discussion, I have assigned the foraging areas reported in the literature for puffins at specific colonies into one of these three foraging habitats. Most reports of foraging areas given in the literature indicate the distance from the colony to which the birds traveled. It should be noted however, that relative distances traveled by birds at different colonies do not necessarily mean that birds at one colony feed further from shore than birds at another colony. The direction of their flight is of equal importance.

Tufted Puffins exhibit considerable variation in the foraging habitats they use, both within a single breeding season at the same colony and between colonies (Wehle, Chapter I). Although they have

been reported feeding in all three habitats during the breeding season, Tufted Puffins in most colonies tend to feed in the inshore waters, at least during the nestling period. At some colonies, there appears to be a correlation between foraging distance and stage of the breeding cycle, with birds feeding in offshore or pelagic waters prior to the onset of the nestling period and thereafter feeding in inshore waters.

Horned Puffins forage primarily in inshore waters throughout the breeding season and almost always closer to shore than Tufted Puffins in areas of sympatry (Wehle, Chapter I).

Most of the information on the foraging habitats of Rhinoceros Auklets and Common Puffins comes from observations made during the nestling period. During this time, both species feed primarily in inshore waters (Rhinoceros Auklet: Heath 1915, Richardson 1961, Cody 1973, Leschner 1976, Hatch et al. 1979; Common Puffin: Kozlova 1957, Corkhill 1973, Ashcroft 1976), although Common Puffins on the Farne Islands, UK, may feed in offshore waters (Pearson 1968). Common Puffins have also been reported feeding in offshore waters during March and April and in inshore waters during June and July (Lockley 1934).

The tendency of all four puffin species to feed in inshore waters, at least during the period in which they carry food to their nestlings, has probably evolved in response to the appearance of shoals of their preferred prey species in inshore waters at that time (Lockley 1934, Pearson 1968, Ashmole 1979, Hart 1973, Straty and Haight 1979).

FOOD OF ADULTS

Primarily within the last 10 years, approximately 277 Tufted Puffins and 155 Horned Puffins have been collected and their stomach contents analyzed and reported as a part of several different studies (Swartz 1966; Sanger and Baird 1977; Sanger et al. 1978; Hunt et al., in prep; Wehle, Chapter I). Prior to these studies, most of the available information on the diet of Tufted and Horned puffins had been either anecdotal in nature or derived from relatively few samples (Heath 1915, Bent 1919; Dement'ev and Gladkov 1951; Kozlova 1957; Bedard 1969; Sealy 1973b, 1973c).

Specific information on the diet of Common Puffins, based on analysis of at least 20 stomachs, is available for the Barents Sea (Belopol'skii 1957), Novaya Zemlya (Uspenski 1958), and Great Britain (Harris and Hislop 1978). General accounts of prey taken by Common Puffins have been afforded by Bent (1919), Witherby et al. (1941), Salomonsen (1950), Kozlova (1957), Kartashev (1960), and others.

Relatively few Rhinoceros Auklet stomachs have been analyzed (Sanger and Baird 1977). Hence, most of the information on the diet of this species comes from descriptive or anecdotal accounts by Bent (1919), Dement'ev and Gladkov (1951), Sealy (1973c), Ashmole (1971), and Bedard (1976) in addition to those summarized by Leschner (1976).

Based on the relative frequency of major food types found in the stomachs of all puffins reported in the aforementioned studies, I have ranked the relative importance of major prey types taken by each species (Table 54). The ratios presented in this table were derived

Table 54. Ratio of the relative importance of major prey types taken by puffins based on the total number of stomachs containing each major prey type.

N				
Tufted Puffin				
280	Fish (18.0) :	Squid (13.0)	: Crustaceans (2.4) :	Polychaetes (1.0)
Horned Puffin				
133	Fish (5.8) :	Squid (3.8)	: Polychaetes (1.5) :	Crustaceans (1.0)
Common Puffin				
117	Fish (16.2) :	Polychaetes (2.3)	: Crustaceans (1.0)	
Rhinoceros Auklet				
	Fish (?) :	Crustaceans (?)		

by dividing the total number of stomachs containing the least common major prey type into the number of stomachs containing each of the other more predominant prey types. Due to the lack of specific analysis of stomach contents for Rhinoceros Auklets, ratios could not be determined; however, the relative importance of major prey types was assessed on the basis of general and anecdotal accounts.

Several general trends in the dietary preferences of puffins are evident from this table: 1) the most important prey type for all puffins is fish, 2) Tufted Puffins consume a considerably greater quantity of fish and squid than crustaceans or polychaetes, while the consumption of these major prey types is more evenly distributed in Horned Puffins, 3) Common Puffins rely much more heavily on fish than on polychaetes or crustaceans, 4) squid are taken in significant amounts by Tufted and Horned puffins, but they are absent in the diet of Common Puffins and possibly also Rhinoceros Auklets, 5) crustaceans are of greater importance to Rhinoceros Auklets than to the other three puffin species.

The majority of fish taken by all puffin species, collectively, are sand lance (Ammodytidae), cod (Gadidae), Capelin (Osmeridae), sculpins (Cottidae) and herring (Clupeidae) (Belopol'skii 1957; Uspenski 1958; Swartz 1966; Leschner 1976; Harris and Hislop 1978; Sanger et al. 1978; Hunt et al., in prep.; Wehle, Chapter I). In general, Tufted Puffins appear to rely more heavily on pelagic or offshore species of fish than the other three puffins, which feed heavily on inshore, subtidal species.

The greater uniformity in the diversity of major prey types taken by Horned Puffins as compared to Tufted and Common puffins suggests that the former species is a more generalized feeder, while the latter two are more specialized. However, all three species exhibit considerable seasonal, yearly, and geographic variation in their diets and are opportunistic in taking advantage of locally or temporarily abundant prey types (Belopol'skii 1957; Harris and Hislop 1978; Sanger et al 1978; Hunt et al., in prep.; Wehle, Chapter I).

I can offer no reasonable explanation for the lack of squid in the diet of Common Puffins. Puffins have been observed rarely to feed squid to their own young on the Isle of May, UK, (Harris and Hislop 1978), and at least three species of terns have been reported feeding cephalopods to their young on the Farne Islands, UK, (Pearson 1968), where puffins also breed.

Finally, stomachs of all species of puffins have been found to contain some type of ingested pollutants. Tufted and Horned puffins in Alaska contained a variety of plastic particles, with the frequency of ingestions being nearly three times greater in Horned than Tufted puffins (Day 1980; Wehle, Chapter I). Although none of the 20 Rhinoceros Auklets collected in Alaska showed evidence of ingested plastic (Day 1980), 1 of 26 of these auklets collected in Monterey Bay, CA, contained plastic (Baltz and Morejohn 1976). Common Puffins have not been reported ingesting plastic but birds examined in different studies contained elastic thread cuttings in their stomachs (Parslow and Jeffries 1972). In all cases, the ingestion of pollutants by puffins apparently has been the result of the birds mistaking the pollutants for natural

prey items. The impact of the ingestion of these pollutants on the physical well-being of puffins remains unknown.

FEEDING AND FOOD OF NESTLINGS

Puffin chicks are dependent solely on their parents for food during the 5 to 8 weeks of their nestling period. Adults capture food for their young by pursuit diving and carry it in their bills back to the nestlings. In the following discussion, I examine several aspects of the feeding ecology of puffin nestlings, including delivery of food, feeding frequency, size and weight of bill loads, prey species composition of bill loads, and size of prey delivered.

Delivery of Food

Puffin chicks are typically fed whole fish, which they swallow head-first; however, there is some evidence that Rhinoceros Auklet chicks are occassionally fed partially digested food by the adults (Jewett et al. 1953, Summers 1970).

Vocalization of chicks just before and during pipping probably stimulates the adults to deliver food to the nest-site (Amaral 1977; Wilson 1977; Wehle, Chapter I). Observations of initial deliveries of food to Horned and Common puffin nestlings indicate that upon entering the nest-site, adults also vocalize, apparently to signify the presence of food (Wehle, Chapter I; Corkhill 1973). Throughout the nestling period, chicks generally vocalize when adults deliver food.

These vocalizations may act to stimulate further feeding by the adults.

Although Common Puffin nestlings may initially take food from the adult's bill (Corkhill 1973), this has not been observed in Tufted and Horned puffins, where adults generally drop the food on the floor of the nest-site to be picked up by the chick (Wehle, Chapter I). The amount of time adult puffins spend in the nest-site when feeding chicks decreases sharply after the first few days. Thereafter, in most cases, the food is dropped at the entrance to the nest-site.

In all four puffin species, both males and females share in the feeding of young. The degree of participation between the sexes is unknown; however, Corkhill (1973) indicated that female Common Puffins may feed more frequently than males.

Feeding Frequency

The temporal pattern of feeding nestlings is similar in all three diurnal species of puffins. Most feeding of young occurs in the early morning with lesser peaks of feeding activity in the early to mid-afternoon and again just prior to nightfall (see Harris and Hislop 1978; Wehle, Chapter I).

The number of feedings per day is extremely variable between days at the same colony, between colonies, and between years. The major factors affecting feeding frequency include the feeding efficiency of the adults, abundance and availability of prey, size and type of prey, weather, and age of the chick. All diurnal puffin nestlings generally receive 2-6 loads of food per day (see Harris and Hislop

1978; Wehle, Chapter I); however, Harris and Hislop (1978) reported the feeding frequency for Common Puffins in some areas varied from 3.8 to 15.7 loads per day, with a maximum of 24.

Unlike the other puffins, Rhinoceros Auklets feed their chicks at night. Auklet nestlings probably receive two deliveries each night (Richardson 1961, Summers 1970, Wilson 1977). The lower number of feedings per day as compared to other puffin species is compensated for by auklets delivering substantially larger loads of food during each delivery (see below).

For the three diurnal species of puffins, the number of feedings per day tends to increase up through the period of peak growth, ending approximately a week prior to fledging (Corkhill 1973, Ashcroft 1976, Amaral 1977, Harris and Hislop 1978). Historically, there has been much controversy over whether or not adult puffins desert or discontinue feeding their young just prior to fledging (Lockley 1934, Perry 1940, Belopol'skii 1957, Myrberget 1962, 1977, Harris 1978). Although a pre-fledging weight recession does appear to be the rule for all puffins, in most cases it is probably the result of voluntary restriction of food intake by the chicks (Summers 1970, Harris 1976b). In some cases, however, adult puffins may actually desert their young (Myrberget 1962) or the adults may cut down on the frequency of feeding prior to the fledging of their chick (Richardson 1961, Ashcroft 1976, Harris and Hislop 1978). Pre-fledging weight recession in alcids may also be due to water loss by maturing tissues (Ricklefs 1968) and/or to increased activity prior to departure (Sealy 1973a).

Size and Weight of Food Loads

Although there is considerable variation between individuals, colonies, and years, each of the three Pacific puffin species typically deliver 3-8 individual prey items per bill load (Wehle, Chapter I; Richardson 1961; Cody 1973; Leschner 1976; Wilson 1977; A. DeGange, pers. comm.). Common Puffins tend to deliver a greater number of prey per load than Pacific puffins. While in most cases Common Puffins average 5-12 prey items per load (Perry 1946, Kartashev 1960, Myrberget 1962, Corkhill 1973, Harris and Hislop 1978), some accounts report averages of nearly twice this number (Salomonsen 1935, Lockley 1953).

The adaptations of the puffin's tongue and bill for the purpose of carrying multiple prey items, especially fish (see Bedard 1969b), are attested to by the maximum number of fish reported in a single load by each species: 29-Tufted Puffin (Cody 1973), 65-Horned Puffin (G. Burrell, pers. comm.), 17-Rhinoceros Auklet (A. DeGange, pers. comm.), and 62-Common Puffin (Harris and Hislop 1978).

The mean weight of bill loads carried by Tufted and Horned puffins is similar, usually 10-20 g, although considerable variation exists (Wehle, Chapter I). Rhinoceros Auklets generally carry heavier loads, averaging about twice that of Tufted and Horned puffins (Richardson 1961, Cody 1973, Leschner 1976, Wilson 1977, Vermeer et al. 1979). The heavier loads delivered by the auklets probably compensate for the fewer number of feedings per day as compared to the other two Pacific puffins. Load weights delivered by Common Puffins

generally average several grams less than those of Tufted and Horned puffins (see Harris and Hislop 1978). Presumably, the lesser amount of food delivered per trip to these chicks is a reflection of the smaller adult body size of Common Puffins.

Although one might suspect that the size and/or weight of bill loads increase throughout the nestling period to meet the progressively greater energy demands of the growing young, neither of these parameters varies consistently between colonies or between years at the same colony. While in some colony-years either or both of these parameters increased (Cody 1973; Corkhill 1973; Wilson 1977; Harris and Hislop 1978; Vermeer et al. 1979; Wehle, Chapter I), in others they decreased (Myrberget 1962; Cody 1973; Leschner 1976; Wilson 1977; Wehle, Chapter I), and in others they were either variable or showed no significant change (Corkhill 1973; Wilson 1977; Harris and Hislop 1978; Wehle, Chapter I).

Species Composition of Food Loads

Both Tufted and Horned puffins feed primarily Pacific Sand Lance (Ammodytes hexapterus) and/or Capelin (Mallotus villosus) to their nestlings; however, the relative importance of subsidiary species tends to be different between the two puffin species (Wehle, Chapter I). In order of importance, Tufted Puffins tend to supplement these two basic prey species with squid and octopus, cod (Gadidae), sculpin (Cottidae), and greenling (Hexagrammidae), whereas Horned Puffins supplement sand lance and Capelin primarily with greenling and cod, and with

lesser amounts of squid and sandfish (Trichodontidae).

Sand lance is also the single most common prey species fed to Rhinoceros Auklet chicks in most colonies and years; however, auklet chicks may also receive relatively large quantities of herring (Clupeidae), anchovy (Engraulidae), and smelt (Osmeridae), and lesser amounts of cod, rockfish (Scorpaenidae), saury (Scomberesocidae), and squid (Heath 1915, Richardson 1961, Cody 1973, Leschner 1976, Leschner and Burrell 1977, Manuwal and Boersma 1978, Wilson 1977, Hatch et al. 1979, Summers and Drent 1979, Vermeer et al. 1979).

Species composition of prey delivered to Common Puffin nestlings has been summarized by Harris and Hislop (1978), who reported that the basic foods of this species are sand lance (Ammodytidae), Sprats (Sprattus sprattus), Herring (Clupea harengus), and a few gadoid fishes, such as Whiting (Merlingius merlangus) and Saithe or Coal-fish (Pollachius virens).

The relative importance of individual prey species in the nestling diet of all four puffin species may show considerable variation throughout the nestling period at the same colony, between colonies in the same year, and between years at the same colony (Wehle, Chapter I; Myrberget 1962; Corkhill 1973; Ashcroft 1976; Leschner 1976; Wilson 1977; Harris and Hislop 1978; Vermeer et al 1979). These variations reflect a concert of factors that influence the abundance and availability of prey species including various aspects of the prey species' natural history (i.e., distribution and movements) and differences in local oceanographic factors (Wehle, Chapter I; Pearson 1968; Wilson 1977; Harris and Hislop 1978).

Although sand lance is the most common prey fed to nestlings by all puffin species, it appears that puffins also select other prey which are less abundant in the water column but which may be of greater nutritional value to the nestlings. In Common Puffins, Harris and Hislop (1978) found that the weights of recently fledged young were significantly higher when sand lance fed to young were supplemented with Sprats rather than Whiting. Similarly, for Tufted and Horned puffins, growth rates of nestlings tended to be higher when sand lance was supplemented with Capelin than with other prey species (Wehle, Chapter I).

Size of Prey

The lengths of prey brought back to nestlings tend to be rather uniform among puffin species and among locations and years. Most fish fed to puffin chicks range in length from 60 to 100 mm, although there is a slight tendency for Common Puffins to feed smaller and Rhinoceros Auklets larger fish than those fed by Tufted and Horned puffins (Wehle, Chapter I; Myrberget 1962; Pearson 1968; Corkhill 1973; Ashcroft 1976; Harris and Hislop 1978; Hatch et al. 1979, A. DeGange, unpub. data).

There is a general tendency for the size of individual fish within a species fed to puffin chicks to increase during the nestling period. Presumably this increase is a result of growth rather than selection of progressively larger prey (Wehle, Chapter I; Myrberget 1962: Harris and Hislop 1978). However, the mean length of all prey species com-

bined may decrease as the season progresses due to selection of different and smaller prey species (Corkhill 1973, Ashcroft 1976). In some cases, the mean length of individual fish within a single prey species may also decrease during the nestling period, possibly as a result of older, larger fish migrating out of the puffin's feeding area while younger, smaller fish migrate into these areas.

Although a few large fish may be a better return for the effort by adult puffins than many small fish, carrying large fish may also impair the flight of the adults and attract cleptoparasitic gulls and jaegers (Harris and Hislop 1978). In captive adult Common Puffins, Swennen and Duiven (1977) found that the maximum size of fish taken was determined by their diameter or height rather than length and that the preferred size was only about 60% of the maximum prey size. These authors suggest that this preference for smaller fish may be related to the greater heat loss incurred by swallowing larger fish. It is likely that this may also be true for other puffin nestlings and that the size of fish delivered to young is a compromise between feeding efficiency of the adults and digestive efficiency/heat loss of the chicks.

SUMMARY AND CONCLUSIONS--CHAPTER II

Four species of puffins exist today: Tufted Puffin (Lunda cirrhata), Horned Puffin (Fratercula corniculata), Common Puffin (F. arctica), and Rhinoceros Auklet (Cerorhinca monocerata). Only the Common Puffin shows subspecific variability. The puffins comprise one of the seven tribes of the family Alcidae, with Cerorhinca in many

ways intermediate between the puffins and the auklets. In the late Pliocene, "Protofratercula" migrated from the center of alcid differentiation in the North Pacific to the North Atlantic and later migrated back to the North Pacific to form two distinct species, F. arctica in the Atlantic and F. corniculata in the Pacific. During the last glaciation and probably also during previous ones, Cerorhinca survived in refuges on both sides of the Pacific but was absent in the Aleutian arc; F. corniculata survived in discontinuous relect populations in the Sea of Okhotsk, the central and eastern Aleutians, and the islands of the Bering Sea (or on the coasts of the Bering Sea land bridge) and Lunda survived along the Pacific coast of North America and in the central area of the Aleutian arc.

Tufted and Horned puffins are sympatric throughout much of their breeding ranges, with Horned Puffins being more abundant in northerly areas than Tufted Puffins. Tufted Puffins breed in the North Pacific from Cape Lisburne, AK, to the Farallon Islands, CA, on the North American coast and from the northern coast of Chukotsk Peninsula, USSR, to Hakkaido, Japan, on the Asian coast. Horned Puffins breed from Cape Lisburne to Forrester Island, AK, on the eastern side of the Pacific and from Wrangel Island to the central Kurile Islands, USSR, on the western side. Both species inhabit the islands of the Bering Sea and the Aleutian chain. Rhinoceros Auklets have the narrowest breeding distribution of the three Pacific puffins. They breed sparingly in the Aleutian and Commander islands and along the Kamchatka Peninsula, and more abundantly south along the North American coast to the Farallon Islands and along the Asian coast to

Korea. Collectively, the three subspecies of Common Puffins breed in Europe on the coasts and associated islands of Greenland, Iceland, Great Britain, Brittany, Norway, and northwestern USSR and, in North America, on the coasts and associated islands from Labrador south to central Maine.

Subadult and adult non-breeding puffins of all four species regularly visit the breeding colonies during the summer, but generally arrive several weeks or more after adults. When not at the breeding colonies, non-breeding Tufted Puffins occur on the open ocean north of the Subarctic Front. Horned Puffins are much less common on the open ocean during this time, apparently remaining closer to shore. Non-breeding Rhinoceros Auklets probably summer in coastal waters within the breeding range of this species. Similarly, most non-breeding Common Puffins remain relatively close to either their natal or associated breeding colonies during this period.

Tufted and Horned puffins winter at sea, generally at latitudes corresponding to the more southerly portions of their breeding ranges. Rhinoceros Auklets, on the other hand, probably winter in inshore waters. Although there appears to be a movement of Rhinoceros Auklets south along the American and Asian coasts in winter, birds breeding in the Aleutian Islands and the Gulf of Alaska probably winter in those areas. The winter distribution of Common Puffins is varied: Some birds remain close to their breeding colonies in the North Sea, others migrate south to the Bay of Biscay and into the western Mediterranean Sea, others range far out to sea and sometimes even cross the Atlantic to North America, and others winter in the Labrador Current and in the Grand Banks.

Recent estimates of puffin population sizes indicate that Common Puffins are the most numerous, with an estimated world population of perhaps 12-15 million birds. The estimated world population of Tufted Puffins is about half that of Common Puffins, and Horned Puffins probably number about half that of Tufted Puffins. The total world population of Rhinoceros Auklets probably number less than 1 million birds.

The preferred nesting habitats of the three Pacific puffin species differ, while those of the Tufted and Common puffin are similar. Both Tufted and Common puffins prefer to nest in earthen burrows along cliff-edges or on steep seaslopes. Only at their extreme northern limit, where frozen ground prohibits burrowing do Common Puffins regularly nest in rock crevices. Rhinoceros Auklets also nest primarily in earthen burrows, but tend to nest in more heavily vegetated areas and on more gradual seaslopes than Tufted Puffins. Horned Puffins nest almost exclusively in rock crevices in talus slopes, under beach boulders, or in cliff-faces. Although the ancestral puffin probably nested in burrows, the current use of rock crevices by Horned Puffins presumably evolved during the time when this species was isolated in high arctic refuges where frozen ground prohibited burrowing. All three diurnal puffin species nest in habitats where they can easily find their nest-sites and can approached and leave them rapidly--important considerations in the face of avian predators and cleptoparasites. These considerations are less important to the nocturnal Rhinoceros Auklet which comes to the breeding colony only at night, when avian predation and cleptoparasitism is minimal. In the

few areas where Rhinoceros Auklets are diurnal, Tufted Puffins are few, thus allowing the auklets to use habitats whose characteristics aid in the avoidance of avian predation and cleptoparasitism.

For each puffin species, there is a positive correlation between arrival time at the breeding colony and latitude, with birds arriving 1-3 mo earlier at their southern than northern breeding limits. The pattern of colony settlement shows considerable interspecific variation among the puffins, but colony settlement is most similar between Tufted and Common puffins.

The interval between arrival and first land-coming for Tufted and Common puffins is usually between 1 and 2 weeks, while that of Horned Puffins is less than 1 week. Tufted and Common puffins, and probably also Rhinoceros Auklets, do not establish continuous occupancy shortly after their arrival as do Horned Puffins, but undergo a quasi-cyclic pattern of colony attendance for a period of several weeks. Generally, the establishment of continuous occupancy and the onset of egg-laying are simultaneous for Tufted and Common puffins, but these events are usually separated by a 2- to 3-week interval in Horned Puffins. The interval between first land-coming and the commencement of egg-laying is approximately a week shorter for Tufted and Common puffins than for Horned Puffins. The marked differences in patterns of colony settlement of Horned Puffins compared to the other three species of puffins probably reflects the evolutionary predilection of the former species to feed in inshore waters and of the other species to feed further offshore.

The length of the pre-egg stage is strongly correlated with latitude for Tufted Puffins but less so for Horned and Common puffins and Rhinoceros Auklets. At the same latitude, the length of the pre-egg stage is slightly longer for Tufted than Horned puffins; and it is generally shorter for Tufted and Horned puffins than for Rhinoceros Auklets and Common Puffins. Variation in the length of the pre-egg stage reflects the interaction of two factors: 1) the availability of food, which is probably more important at southern range limits, and 2) the accessibility of nest-sites, which is more important at northern range limits. That the length of the pre-egg stage is generally shorter for Tufted and Horned puffins than for Common Puffins and Rhinoceros Auklets is probably due to the fact that throughout much of the breeding range of the former two species, the two controlling factors (the availability of food and the accessibility of nest-sites) coincide to a greater extent than they do in the more southerly regions of the Pacific or in the North Atlantic where the latter two species breed.

The sexes of all puffin species are essentially monomorphic, although males tend to be slightly larger than females. Puffins undergo an incomplete prenuptial molt which provides them with adornments important in courtship. All four puffin species share a number of behaviors in common: billing, fly-bys, fighting, head-dipping, wing-flapping, and preening. Other behaviors, such as the courtship ceremony, head-jerking, bowed-head display, landing display, and bill-gaping show some interspecific variability between Tufted, Horned, and Common puffins but have not been described for Rhinoceros Auklets.

Tufted and Common puffins, and probably Rhinoceros Auklets, establish nest-sites by territorial antagonistic behavior among males. Each of these species defends an area in the immediate vicinity of the nest-site, including the nest-site entrance, approach path, and landing/take-off/loafing sites. Male Horned Puffins may also establish nest-sites by territorial antagonistic behavior, but this species probably only defends the nest itself.

Tufted and Horned puffins have four vocalizations in common, although each vocalization shows some degree of interspecific variability: a single note call, a purring call, a bi-syllabic call, and a multi-note call. Each of these four vocalizations resemble, at least superficially, vocalizations reported for Common Puffins. Published descriptions of the vocalizations of Rhinoceros Auklets are few, but this species appears to have at least two vocalizations (the single note call and the multi-note call) that are similar to those of the other three species.

Because burrows are more subject to structural damage by environmental forces over the winter than are rock crevices, the three burrow nesting puffin species spend more time preparing their nest-site for egg deposition each spring than Horned Puffins. All four species, however, thoroughly clean their nest-sites each year. In general, new burrows are not excavated in the same year in which they are used for breeding. All puffin species construct nests usually within several days preceding egg-laying. Nesting material typically consists of grasses and feathers but may contain a variety of other materials.

Nest-site tenacity has been demonstrated in Tufted and Common puffins and in Rhinoceros Auklets and is strongly suspected in Horned Puffins. Selection favoring nest-site tenacity in puffins has apparently occurred to facilitate the occupancy of nest-sites where the length of the breeding season is relatively short as a result of climate-related factors.

The degree of interspecific competition potentially encountered by each puffin species depends chiefly on two factors: the number and abundance of other sympatric species which may compete for the same nest-sites and the availability of suitable nest-sites. Thus, the potential for interspecific competition for each species varies between colonies. Tufted and Common puffins and Rhinoceros Auklets sometimes cohabit nest-sites with other species. Generally, cohabitation occurs only between a diurnal and a nocturnal species--a mechanism apparently evolved to reduce interspecific competition. Because of the inaccessibility of most Horned Puffin nest-sites to observation, there are few reports of cohabitation in this species; however, in light of the large number of species which nest in rock crevices, it is likely that such cohabitation occurs.

The onset of egg-laying in puffins occurs 2-5 weeks later at their northern than southern breeding limits, although local conditions may cause variations from this general pattern. In areas of sympatry, peak egg-laying of Tufted Puffins generally coincides with that of Rhinoceros Auklets but occurs approximately 1-2 weeks earlier than for Horned Puffins. Intracolony variation in the timing of egg-laying has been attributed to breeding experience and the use of optimal versus

sub-optimal habitat. Data concerning the relative timing of laying among pairs in the same colony are conflicting.

Puffin eggs are ovate in shape and are dull creamy-white or pale bluish-white with various amounts of spots and/or scrawls of gray, blue, green, reddish-brown, and brown. Tufted Puffin eggs are significantly larger than Horned Puffin eggs. Horned Puffin and Rhinoceros Auklet eggs tend to overlap in size, though the latter are slightly larger on the average. Common Puffins lay the smallest eggs of any puffins. Proportionate egg weight in the four puffin species ranges from 9.5% to 15.5%.

Most puffins apparently lay a replacement egg if the first egg is deserted or lost. Egg replacement time ranges from 1.5 to 3 weeks. Although selection has favored replacement laying in puffins, local conditions, especially proximity to sufficient food resources, exerts a strong influence on whether puffins will lay replacement clutches in any particular colony or year.

Incubation is shared by both sexes in all puffin species. In general, the sexes exchange incubation duties at least once daily, but single shifts of a day or longer have been reported for each species. Similarly, all puffins frequently leave their eggs unattended for several hours a day and Tufted and Horned puffins and Rhinoceros Auklets may temporarily desert their eggs for several days. Like a number of other seabirds, puffin eggs are able to withstand considerable chilling--an adaptation in birds which feed offshore or whose food supply is patchily distributed.

The mean lengths of incubation for Tufted Puffins and Rhinoceros Auklets are several days longer than for Horned and Common puffins. The slower embryo growth rate in the former two species is probably advantageous in that these species typically feed farther from the breeding colonies than either Horned or Common puffins. Also, Tufted Puffins and Rhinoceros Auklets both exhibit a greater degree of variability in their length of incubation than the other two species.

Young puffins hatch with the aid of a single egg tooth located on the tip of the upper mandible. In Tufted and Horned puffins, the egg tooth tends to disappear gradually within several weeks after hatching, but in Rhinoceros Auklets the egg tooth is deciduous, dropping off within a week after hatching. Egg tooth retention time in Common Puffins has not been reported but is probably similar to that of Tufted and Horned puffins.

After hatching, Tufted Puffins and Rhinoceros Auklets brood their chicks more or less continuously for 1-3 days, while Horned and Common puffins brood for 5-7 days. The shorter brooding period of Tufted Puffins and Rhinoceros Auklets appears to be an adaptation in those species feeding farthest from the breeding colony.

Puffins have a semi-precocial post-hatching development pattern in which the young are fed in the nest until they are at least two-thirds of adult body-size and in complete juvenal plumage. Although there is considerable inter- and intraspecific variation in the length of the nestling period, nestling period length is generally longer in Tufted Puffins and Rhinoceros Auklets than in Horned and Common puffins. Longer nestling periods are correlated with slower growth

rates of chicks, again an adaptation to those species feeding on distant or patchily distributed food supplies.

In most colony-years, laying success of Tufted Puffins has been 50-60%. In two colony-years studied, Rhinoceros Auklets had a laying success of 62% and 65%. Specific data on the laying success of Common Puffins are not available, but a proportion of pairs on the colonies have been reported to occupy nest-sites but not lay eggs.

Most reported values of hatching success for puffins are probably lower than they would have been under natural conditions as a result of human disturbance. Puffins probably have a natural desertion rate of 5-20%. The main causes of egg mortality in puffins are 1) desertion or loss from disturbance by other birds or animals, 2) desertion or inviability related to weather, 3) infertility, and 4) predation. In general, hatching success of all puffin species under natural conditions is probably 75-90%.

For all colony-years reported, the average fledging success was 60-70% for Tufted Puffins, 53-77% for Horned Puffins, 82% for Rhinoceros Aklets, and 72% for Common Puffins. Interspecific variation in fledging success among colony-years is correlated with weather, food availability, predation, and cleptoparasitism. Most puffin chick mortality occurs within the first 2 weeks after hatching, with later mortality being primarily the result of starvation.

Values of total breeding success in puffins has varied from 0.9% to 90.5%. Although a variety of factors affect total breeding success, the single most important factor is food availability.

At least 13 species of birds and five species of mammals prey on the four species of puffins. In addition, it is also likely that puffins are regularly eaten by several species of marine fish. Although adult puffins may comprise a significant proportion of the diet of certain predators in some colonies, mortality of adult puffins by predation is probably minimal in most colonies.

At least eight species of birds are cleptoparasites of puffins. In some areas, cleptoparasitism of adult Common Puffins significantly reduced fledging success; however, cleptoparasitism of this magnitude has not been reported in Pacific puffin colonies.

Puffins capture their prey by pursuit diving and probably take most of their prey within 15 m of the surface. In general, puffins feed singly but may also feed in monospecific or mixed species assemblages. Possible intraspecific cooperation in feeding among Common Puffins has been suggested by Ashcroft (1976). Of the four puffin species, Tufted Puffins exhibit the greatest variability in foraging habitats used during the breeding season, feeding in oceanic, offshore, and inshore waters. In most colonies, Tufted Puffins tend to feed in inshore waters during the nestling period. Horned Puffins forage primarily in inshore waters throughout the breeding season and almost always closer to shore than Tufted Puffins in areas of sympatry. Because of their nocturnal habits, little information is available on foraging habitats used throughout the breeding season by Rhinoceros Auklets; however, they tend to feed in inshore waters during the nestling period. Common Puffins also tend to feed in inshore waters during the nesting stage but sometimes feed in offshore waters

during this and earlier stages of the breeding period. The tendency of all four puffins species to feed in inshore waters at least during the nestling period, has probably evolved in response to the appearance of fish shoals in inshore waters at that time.

The most important prey type taken by all puffin species is fish. Tufted Puffins appear to rely more heavily on pelagic or offshore species of fish than the other three puffins which feed on inshore, subtidal species. Tufted Puffins consume a considerably greater quantity of fish and squid than crustaceans and polychaetes, while the consumption of these four major prey types is more evenly distributed in Horned Puffins. Common Puffins rely much more heavily on fish than on polychaetes or crustaceans. Common Puffins and possibly also Rhinoceros Auklets apparently do not feed on squid. Rhinoceros Auklets consume relatively greater amounts of crustaceans than do the other three puffin species. Although Horned Puffins appear to be more generalized feeders than Tufted or Common puffins, all three species exhibit considerable seasonal, yearly, and geographic variation in their diets and are opportunistic in taking advantage of locally or temporarily abundant prey types.

All four puffin species have been found to contain some type of ingested pollutants--plastic particles in Tufted and Horned Puffins and Rhinoceros Auklets, and elastic thread cuttings in Common Puffins. The ingestion of these foreign substances apparently occurs as the result of birds mistaking them for natural prey.

Puffin chicks are dependent solely on their parents for food during the 5 to 8 weeks of their nestling period. Adults of both

sexes carry food in their bills back to their nestlings. There is some evidence that Rhinoceros Auklet chicks are occasionally fed partially digested food by the adults.

In the three diurnal puffins, most food deliveries occur in the early morning with fewer deliveries in the early to mid-afternon and again just prior to nightfall. In general, puffin chicks of diurnal species receive two to six loads of food each day, the number tending to increase with chick age. In the nocturnal Rhinoceros Auklet, chicks probably receive two loads of food each night. Although a pre-fledging weight recession appears to be the rule for all puffins, in most cases it is probably the result of voluntary restriction of food intake by the chicks rather than restriction of feeding by the adults.

There is considerable variation in the size of loads delivered to chicks among individuals, colonies, and years, but each of the three Pacific puffin species typically deliver three to eight individual prey items per bill load. Common Puffins tend to deliver a greater number of prey per load of five to twelve items. The mean weight of bill loads delivered by Tufted and Horned puffins is similar, usually 10-20 g. Rhinoceros Auklets deliver bill loads of about twice this weight, while Common Puffin bill loads average several grams less than for Tufted and Horned puffins. There does not appear to be any general trend to increase the size and/or weight of bill loads during the nestling period.

Sand lance is the single most common prey fed to nestlings of all four puffin species throughout their ranges. Both Tufted and Horned

puffins also rely heavily on Capelin but differ in their choice of secondary prey species. Rhinoceros Auklets supplement sand lance with large amounts of herring, anchovy, and smelt and lesser quantities of cod, rockfish, saury, and squid. Other than sand lance, the major foods of Common Puffin nestlings are Sprats, herring, and a few gadoid fishes, such as Whiting and Saithe or Coalfish. The relative importance of individual prey species in the diet of all four puffin species shows considerable variation throughout the nestling period at the same colony, between colonies in the same year, and between years at the same colony.

Most fish fed to puffin chicks range in length from 60 to 100 mm, though there is a slight tendency for Common Puffins to feed smaller and Rhinoceros Auklets larger fish than those fed by Tufted and Horned puffins.

CONCLUSIONS

In Chapter I, I presented new data from a variety of recent Tufted and Horned puffin studies and summarized the available information concerning the ecology of these two species. In Chapter II, I compared the information presented in Chapter I with that available for Rhinoceros Auklets and Common Puffins to provide a synthesis of the natural history of the world's four species of puffins. It is hoped that the information presented in these chapters will be used to assess the potential impact of and to establish guidelines for future resource development in areas inhabited by puffins.

The development of resources, especially petrochemical, in these areas poses potential threats to the well-being of all four puffin species. These threats include the short-term, direct mortality of birds by events such as oil spills, the ingestion of lethal pollutants, or the introduction of predators (e.g., rats) and also the long-term decline of population numbers by causes such as the reduction in the availability and/or abundance of prey, the destruction of nesting habitat, or the discontinuance of breeding activities as a result of human disturbance on the colonies.

One might suspect that short-term, direct mortality of birds is relatively easy to document; however, this may not always be the case (see Hope Jones 1965, Monnat 1969, Cramp et al. 1974). Also, it is difficult to detect long-term population declines and as difficult to identify the cause(s) of such declines (see Cramp et al. 1974, Harris

1976). Thus, possible detrimental effects of resource development on puffins are difficult to document even after the fact. Therefore, management aimed at the conservation of puffins requires the prediction of potential conflicts between resource development and puffin well-being, coupled with the establishment of safeguards to prevent these conflicts from becoming reality. The identification of potential conflicts, in turn, depends on the type of resource development. While it would be impossible in this paper to identify all potential conflicts for all types of resource development, the following fundamental aspects of puffin natural history should be considered in all future management decisions:

1) Puffins are present at or in the vicinity of the breeding colonies approximately 4.5 mo each year.
2) Tufted, Horned, and Common puffins are diurnal at the breeding colonies; Rhinoceros Auklets are nocturnal.
3) Puffins nest primarily in earthen burrows or rock crevices on offshore islands or isolated headlands.
4) Puffin burrows are very susceptible to structural damage by weather-related factors and trampling by terrestrial mammals.
5) Burrow nesting puffins are particularly susceptible to predation by terrestrial predators.
6) In some colonies, there may be keen inter- and intraspecific competition for nest-sites.
7) Puffins are extremely prone to desertion of their nest-sites during the pre-egg and egg stages of the breeding cycle.

8) Puffins probably do not breed until they are at least 4 or 5 yrs. old.

9) A relatively large proportion (perhaps 50%) of puffins present on the breeding colonies at any time are not reproductively active.

10) Puffins generally lay only one egg each year, but may lay a replacement egg if the first egg is lost or deserted relatively early during incubation.

11) Generally, only 20-50% of the puffin pairs which occupy nest-sites during the pre-egg stage fledge young.

12) Puffins occur over a broad expanse of the North Pacific and North Atlantic oceans throughout the year, especially in winter.

13) During the breeding season, puffins may feed in oceanic, offshore, and/or inshore waters; but, all species tend to feed inshore during the nestling period.

14) Puffins are opportunistic in their feeding, taking advantage of locally or temporarily abundant prey.

15) Adult Tufted Puffins rely more heavily on pelagic or offshore species of fish than adults of the other three species, which feed on inshore, subtidal species.

16) The most important prey taken by adult puffins of all species is fish, although squid, polychaetes, and crustaceans may also make up a significant portion of their diets.

17) Adults of all puffin species have recently been found to contain some form of ingested pollutants, especially plastic. The effect of these pollutants on the well-being of the birds has not been determined.

18) Puffin chicks are solely dependent on their parents for food during the 5-8 weeks of their nestling period.

19) Sand lance (Ammodytes spp.) is the single most common prey fed to nestlings of all puffin species.

20) Growth rates of Tufted and Horned puffin nestlings are highest when both sand lance and Capelin (Mallotus villosus) comprise at least 85-90% of all prey fed to nestlings. Similarly, growth rates of Common Puffin nestlings are highest when sand lance is supplemented with Sprats (Sprattus sprattus).

These fundamental aspects of puffin natural history warrant the following general safeguards with respect to puffin conservation:

1) Human activity of any type (except as indicated below) should be prohibited within a puffin colony during the breeding season. Activity conducted at other times should be conducted in such a manner that the nesting habitat of the birds is not damaged.

2) Domestic animals should be prohibited within a puffin colony at all times of the year.

3) Populations of puffin prey species, especially sand lance, Capelin, and Sprats, should not be affected in any manner which would adversely affect puffin feeding ecology, e.g., by commercial fishing, pollution, or habitat destruction.

4) Collecting of puffins and their eggs should be limited to supervised subsistence hunting by native peoples and to scientific investigations.

Although our knowledge of puffin natural history has increased greatly in recent years, much more needs to be learned to both ac-

curately assess the impact of resource development conflicts with puffins and to make informed management decisions regarding puffins. To achieve these capabilities, studies in the following areas are recommended:

1) population dynamics of Pacific puffins: post-fledgling, immature, and adult annual and seasonal survival rates; population age and sex structure.
2) breeding biology of Pacific puffins: degree of philopatry, nest-site tenacity, and mate fidelity; reproductive longevity.
3) winter biology of all puffins: distribution, movements, food and feeding.
4) food and feeding ecology of adult and nestling puffins: yearly, seasonal, and geographic variation in prey species abundance and availability; the effect this variation has on puffin breeding biology; selectivity of prey in the water column by puffins, i.e., what prey are taken by puffins relative to what is available.

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APPENDICES

Appendix 1. Breeding chronology of puffins throughout their ranges.

Location	Coordinates	Year	Arrival: First	Arrival: Peak	First Land-crowding	Egg-Laying: Peak	Egg-Laying: Range	Hatching: Peak	Hatching: Range
TUFTED PUFFIN									
Farallone Is., CA	37°40'N 123°00'W			late Mar		27 May-17 June			
Vladivostok, USSR	43°06'N 131°48'E			early Apr					
Ussuysk I., USSR	44°00'N 131°00'E			early Apr			late May-	early July	
Destruction I., WA	47°40'N 124°24'W	1974		13 Apr	20 Apr		late May-late June		
		1975				6-9 May			21 June-24 July
Tetangis I., B C.	50°52'N 128°05'W	1915				9 June		mid-July	
		1977				26 May		late July	
Buldir I., AK	52°21'N 176°54'E	1975	17 May (p)		23 May	5-10 June	5 June-	19 July-2 Aug	
Forrester I., AK	54°48'N 133°31'W	1976					20 May-5 June		5-21 July
Commander Is., USSR	55°56'N 167°13'E		5 May (p)			late June-early July		early Aug	
Shumagin Is., AK	55°22'N 159°20'W	1976	7 May (p)			25 May-5 June	25 May-23 June	9-15 July	
Nelson Lagoon, AK	56°00'N 161°10'W	1977	8 May	15-30 May			late May-late June		
Chowiet I., AK	56°02'N 156°45'W	1976					25 May-30 June	19 July	9 July-24 Aug
St. George I., AK	56°30'N 169°40'W	1977			27 May				
Ugamashak I., AK	56°47'N 156°41'W	1976	24 May (p)			1-11 June	31 May-	17-20 July	
		1977	10 May			4-14 June	4 June-	20 July-1 Aug	
Sitkalidak I., AK	57°05'N 153°20'W	1977				3-12 June	23 May-24 June	30-24 July	7 July-8 Aug
St. Paul I., AK	57°10'N 170°20'W	1911-15	15-20 May			mid-June-early July			
		1977	21 May						
Barren Is., AK	58°55'N 152°10'W	1976	14 May (p)			1-15 June	28 May-24 June	10-31 July	
		1977	20 May (p)			30 May-12 June	27 May-18 June	31 July-6 Aug	
Middleton I., AK	59°35'N 146°35'W	1978				16-28 May	12 May-15 June		27 June-29 July
St. Lawrence I., AK	63°10'N 172°12'W	1952	4 June						
		1958	23 May						
		1966	23 May						
		1967	26 May						
Little Diomede I., AK	65°45'N 168°55'W	1952	2 June						
		1958	26 May		13 June				
Cape Thompson, AK	68°08'N 166°00'W	1960	11 June						
		1961	8 June						
HORNED PUFFIN									
Anderson I., USSR	66°00'N 142°00'E			early May					
Buldir I., AK	52°21'N 176°56'E	1975	17 May (p)		25 May	13-20 June	5-30 June	23-30 July	
Forrester I., AK	54°48'N 133°31'W					20-30 June			mid-July-
Shumagin Is., AK	55°22'N 159°20'W	1976	7-26 May		2 June	25 June	10 June-4 July	5 Aug	20 July-14 Aug
Chowiet I., AK	56°02'N 156°45'W	1976	29 May		30 May		25 May-30 June	31 July	23 July- 17 Aug
		1977	20 May						
St. George I., AK	56°30'N 169°40'W		9-21 May						
		1177							
Ugamashak I., AK	56°47'N 156°41'W	1976	31 May		1 June	1-11 June	31 May-	30 July-6 Aug	
		1977	20 May	27 May	27 May	4-14 June	4 June-	25-30 July	
St. Paul I., AK	57°10'N 170°20'W		9-10 May			19 June-1 July			
		1977			26 May		22 June-10 July		early-mid Aug
Barren Is., AK	58°55'N 152°10'W	1976	10 May		24 May	14-20 June		22-31 July	
		1977	25 May		28 May	12-21 June		21 July-10 Aug	
St. Lawrence I., AK	63°10'N 172°12'W	1952-56	15-22 May						
		1966	26 May						
		1967	28 May			29 June	24 June-	30 July-6 Aug	
Little Diomede I., AK	65°45'N 168°55'W	1953	2 June				after 25 June		
		1958	2 June						
Cape Thompson, AK	68°08'N 166°00'W	1960	6 June				25 June-	mid-Aug	
		1961	8 June				4 July-		

Appendix I. Continued

Location	Coordinates	Year	Fledging Peak	Range	Departure	Source
TUFTED PUFFIN						
Farallon Is., CA	37°40'N 123°00'W					Grinnell and Wythe (1927)
Vladivistok, USSR	43°06'N 131°47'E					Kozlova (1957)
Kruppa I., USSR	46°06'N 151°00'E					Kozlova (1957)
Destruction I., WA	47°40'N 124°24'W	1974				Fraser (1975)
		1975				G. Burrell (pers. comm.)
Triangle I., B.C.	50°52'N 128°05'W	1975	25 Aug -8 Sept	12 Aug.-22 Sept		Vermeer et al. (1975)
		1977				Vermeer et al. (1978)
Bubilr I., AK	54°21'N 176°56'E	1975		late Sept -	5 Sept (p)	this study, Chapter I
Forrester I., AK	54°48'N 133°31'W	1976			1 Sept (p)	Delange et al. (1977)
Commander Is., USSR	55°04'N 167°13'E		late Sept			Stejneger (1885) Kozlova (1957)
Shumagin Is., AK	55°22'N 159°30'W	1976				Moe and Day (1978)
Nelson Lagoon, AK	56°00'N 161°10'W	1977		late Aug -early Sept		R. Gill (pers. comm.)
Chowiet I., AK	56°02'N 156°45'W	1976		4 Sept.-		Leschner and Burrell (1977)
St. George I., AK	56°30'N 169°40'W	1977			21 Sept (p)	Hunt et al. (1978)
Ugaiushak I., AK	56°47'N 156°41'W	1976		27 Aug. -	2 Sept (p)	this study, Chapter I
		1977		27 Aug	29 Aug (p)	this study, Chapter I
Sitkalidak I., AK	57°05'N 153°20'W	1977		25 Aug -	11 Sept (dg)	Baird and Moe (1978)
St. Paul I., AK	57°10'N 170°20'W	1911-15		-2 Oct		Preble and McAtee (1923)
		1977			21 Sept (p)	Hunt (1978)
Barran Is., AK	56°55'N 152°10'W	1976		26 Aug -		Amaral (1977)
		1977				Manuwal and Boersma (1978)
Middleton I., AK	59°25'N 146°35'W	1978		12 Aug.-14 Sept		Hatch et al. (1979)
St. Lawrence I., AK	63°10'N 172°12'W	1952				Sealy (1973b)
		1958				"
		1966			14 Sept (p)	"
		1967			9 Sept (p)	"
Little Diomede I., AK	65°45'N 168°55'W	1953				Kenyon and Brooks (1960)
		1958				"
Cape Thompson, AK	68°02'N 166°00'W	1960			25 Sept (la)	Swartz (1966)
		1961			23 Sept (la)	"
HORNED PUFFIN						
Moneron I., USSR	45°00'N 142°00'E		1-10 Sept.			Kozlova (1957)
Bubilr I., AK	52°21'N 176°56'E	1975		late Sept -	5 Sept (p)	this study, Chapter I
Forrester I., AK	54°48'N 133°31'W					Willett (1915)
Shumagin Is., AK	55°22'N 159°30'W	1976		after 3 Sept -		Moe and Day (1977)
Chowiet I., AK	56°02'N 156°45'W	1976		after 4 Sept -		Leschner and Burrell (1977)
		1977				Hatch (1978)
St. George I., AK	56°30'N 169°40'W					Preble and McAtee (1923)
		1977		13 Sept -	21 Sept (p)	Hunt et al. (1978)
Ugaiushak I., AK	56°47'N 156°41'W	1976		early Sept	2 Sept (p)	this study, Chapter I
		1977		early Sept	29 Aug (p)	this study, Chapter I
St. Paul I., AK	57°10'N 170°20'W					Preble and McAtee (1923)
		1977				Hunt (1978)
Barran Is., AK	56°55'N 152°10'W	1976		4 Sept -		Amaral (1977)
		1977				Manuwal and Boersma (1978)
St. Lawrence I., AK	63°10'N 172°12'W	1952-54				Sealy (1973b)
		1966			14 Sept (p)	"
		1967		7 Sept -	9 Sept (p)	"
Little Diomede I., AK	65°45'N 168°55'W	1953				Kenyon and Brooks (1960)
		1958				"
Cape Thompson, AK	68°08'N 166°00'W	1960		7 Sept -	27 Sept -2 Oct.	Swartz (1966)
		1961		24-27 Sept -	24 Sept (la)	"

Appendix I. Continued

Location	Coordinates	Year	Arrival: First	Arrival: Peak	First Land-sighting	Egg-Laying: Peak	Egg-Laying: Range	Hatching: Peak	Hatching: Range
RHINOCEROS AUKLET									
Moneron I., USSR	44°06'N 142°00'W			late Mar -early Apr			early May-		
Destruction I., WA	47°40'N 124°24'W	1974				7-25 May	7 May-13 June		
		1975		Apr.		2-17 May	2 May-17 June		
Protection I., WA	48°08'N 122°55'W		late Feb -early Mar			early May	21 Apr -31 May		late May-late June
		1935				4-26 May	30 Apr.-2 June		17 June-17 July
		1976				10 May-3 June	2 May-16 June		16 June-27 July
Smith I , WA	48°21'N 122°51'W	1974					10 May-7 June		20 June-15 July
Cleland I., B.C.	49°10'N 126°10'W	1969		late Apr -early May		28 Apr -10 May		9-21 June	-12 July
Triangle I , B.C.	50°52'N 128°05'W	1975							
		1976							1-22 July
		1977							
		1978							10 June-15 July
Forrester I., AK	54°48'N 133°31'W	1913				1-15 June		1-7 July	27 June-
		1914					late May-late June		
		1976					26 May-24 June		5 July-4 Aug
Chowiet I., AK	56°02'N 156°52'W	1976					late May-17 June	16 July	
Middleton I., AK	59°25'N 146°35'W	1978				26 Apr -20 May	22 Apr -3 June		7 June-9 July
COMMON PUFFIN									
Machias Seal I., ME	44°30'N 67°06'W	1939	5 Apr				11 May-		
Great I., Newfoundland	47°11'N 52°46'W		12 Apr		17 Apr	13-28 May	5 May-13 June	late June-early July	
Lundy I., U.K.	51°12'N 04°50'W		28 Mar		late Mar -early Apr	mid-May	8 May-		16 June
Skokholm, U.K.	51°42'N 05°16'W	1928	28 Mar		4 Apr				
		1929	25 Mar		6 Apr				
		1930	31 Mar		8 Apr				
		1931	25 Mar		8 Apr				
		1932	22 Mar		4 Apr				
		1933	29 Mar		3 Apr	early May	26 Apr -16 May	mid-June	
Skomer I., U.K.	51°44'N 15°19'W	1932-76	late Mar		early Apr				
		1910				1-21 May	27 Apr -30 May		
		1974				14-28 May			
		1975				30 Apr -12 May			
Isle of May, U.K.	56°12'N 02°32'W	1936	early Mar		28 Mar	14-28 Apr	13 Apr -2 June	3 June	14 May-13 July
Orkney Is., U.K.	59°01'N 02°08'W		early-mid Apr		14-22 Apr				
Shetland Is., U.K.	60°35'N 03°10'W					9-16 May			
Iceland	63°12'N 19°43'W			19-20 Apr		11-14 June	22 May-16 June		
Eysundsan, Norway	66°20'N 12°12'E	1955				2-12 June	26 May-21 June		
		1956		1-18 Apr		19 May-1 June	17 May-24 June		
Ainovy Is., USSR		1948				14-23 May	13 May-5 June		
		1950				10-20 May	8 May-10 June		
Bavan Is., USSR	68° N 35° E	1935				6-18 June	23 May-13 July		
		1938					7 June-		12 July-
		1939					31 May-		
		1947				21 May-10 June	14 May-15 June		18 June-
		1948				23 May-5 June	21 May-17 June		25 June-
		1949				27 May-18 June	26 May-20 June		30 June-
		1950				12 May-1 June	11 May-15 June		15 June-
Kharlov I., USSR	66° N 37° E	1931-40					late May-mid-July	4-12 July	
Githcraye Bay, USSR	72°00'N 54°46'E		mid-May				late June-early July	early Aug	
Greenland	74° N 40° W		8-10 May			early-mid-June			

Appendix I. Continued

Location	Coordinates	Year	Fledging Peak	Range	Departure	Source
BIBULICHUS AURILET						
Moneron I., USSR	46°00'N 142°00'W					Kozlova (1957)
Destruction I., WA	47°40'N 124°24'W	1974				Leschner (1976)
		1975				"
Protection I., WA	48°08'N 123°55'W		early Aug		late Aug	Richardson (1961)
		1975		3 Aug.-6 Sept.		Wilson (1977)
		1976		11 Aug.-12 Sept.		"
Smith I., WA	48°21'N 122°51'W	1974		11 Aug.-29 Aug.		Manuwal (unpub. data)
Chirinol I., B.C.	49°10'N 126°10'W	1969	29 July-15 Aug	23 July-27 Aug		Summers (1970), Summers and Drent (1979)
Triangle I., B.C.	50°52'N 128°05'W	1975	12-20 Aug	12 Aug.-10 Sept.		Vermeer et al. (1979)
		1976	26 Aug.-2 Sept	12 Aug.-16 Sept		"
		1977	19-26 Aug	12 Aug.-9 Sept.		"
		1978	12-19 Aug	29 July-2 Sept.		"
Forrester I., AK	54°48'N 133°31'W	1913		6 Aug		Heath (1915)
		1914				Willett (1915)
		1916		27 Aug.-	1 Sept (p)	Degange et al. (1977)
Chowiet I., AK	56°02'N 156°45'W	1976		19 Aug.-		Leschner and Burrell (1977)
Middleton I., AK	59°25'N 146°31'W	1978		14 Aug.-12 Sept		Hatch et al. (1979)
CERORCH PUFFIN						
Matinicus Seal I., ME	43°30'N 67°06'W	1879		15 Aug -	mid-Aug -early Sept.	B. Howell (pers.comm.)
Great I., Newfoundland	47°31'N 52°45'W			early Aug.-late Sept		Nettleship (1972)
Lundy I., U.K.	51°12'N 05°50'W				late July-early Aug	Perry (1940, 1975)
Skokholm, U.K.	51°42'N 05°16'W	1828			22 Aug -7 Sept	Lockley (1934)
		1929			16 Aug -12 Sept	"
		1930			16 Aug -10 Sept.	"
		1931			15 Aug -17 Sept	"
		1932			24 Aug -18 Sept	"
		1933	late July-early Aug		26 Aug -6 Sept	"
Skomer I., U.K.	51°44'N 15°15'W	1972-76			early Aug	Ashcroft (1976)
		1970				Corkhill (1972)
		1974				Ashcroft (1976)
		1975				"
Isle of Man, U.K.	54°12'N 02°32'W	1978		5 July-9 Aug	early-mid-Aug	M.P. Harris (pers.comm.), Wade (pers.obs.)
Orkney Is., U.K.	59°01'N 02°08'W					Perry (1948)
Shetland Is., U.K.	60°31'N 02°32'W					"
Iceland	65°12'N 19°45'W					Kautashev (1960), Bent (1919)
Lovunden, Norway	66°20'N 12°12'E	1955	mid-late Aug			Myrberget (1962)
		1956	late-Aug.-early Sept			"
Alaverg Is., USSR		1969				Belopol'skii (1957)
		1950				"
Seven Is., UbGR	68° N 35° E	1935		9 Aug -		Belopol'skii (1957)
		1938		24 Aug -		"
		1939		16 Aug -		"
		1947		31 July-		"
		1948		7 Aug -		"
		1949		10 Aug -		"
		1950		28 July-		"
Kharlov I., USSR	68° N 37° E	1939-40	20 Aug	early-late Aug		Kozlova (1957)
Gillaveya Bay, USSR	72°08'N 54°46'E				mid-Sept	Uspenski (1958)
Greenland	74° N 60° W			late Aug -early Sept		Salomonsen (1950)

p=present, eg=nestly gone, la=last seen

...by settlement during the pre-egg stage of Tufted and Horned puffins, Rhinoceros Auklets, and Common Puffins throughout their ranges.

Coordinates	Year	Interval between arrival and first land-coming	Interval between arrival and continuous occupancy	Interval between first land-coming and continuous occupancy	Interval between continuous occupancy and start of egg-laying	Interval between first land-coming and start of egg-laying	Interval between arrival and start of egg-laying	Source
37°40'N 123°00'W							c. 2 months	Grinnell and Wythe (1927)
46°00'N 151°00'E			30 days		c. 0 days		4-6 weeks	Kozlova (1957)
47°40'N 124°24'W	1974	7 days	30 days	24 days	1 week	c. 4 weeks	5-6 weeks	Fraser (1975)
52°21'N 176°56'E	1975	6 days	14 days	38 days		13 days	19 days	this study, Chapter I
53°08'N 173°18'E	1974	9 days						J. L. Trapp (pers. comm.)
55° N 163° E		c. 10 days						Dement'ev and Gladkov (1951)
55°20'N 166°00'E							c. 6 weeks	Stejneger (1958)
55°22'N 159°20'W	1976						19 days	Moe and Day (1979)
56°00'N 161°10'W							3 weeks	R. Gill (pers. comm.)
56°47'N 151°41'W	1976		24 days	24 days	0 or 1 days	25 days	25 days	this study, Chapter I
	1977	0 days	26 days	26 days	0 days	25 days	25 days	this study, Chapter I
57° N 163°20'W							c. 1 month	Preble and McAtee (1923)
58°55'N 152°10'W	1976	7 days	6 days	0 days	8 days	9 days	2 weeks	Amaral (1977)
	1977						8 days	Manuwal and Boersma (1978)
53°10'N 172°12'W		c. 7 days					c. 3 weeks	Sealy (1973b)
55°10'N 176°12'W		18 days						Kenyon and Brooks (1960)
52°21'N 175°56'E	1975	8 days	8 days	2 days	11 days	13 days	19 days	this study, Chapter I
53°08'N 173°18'E	1974	0 days						J. L. Trapp (pers. comm.)
55°22'N 159°20'W	1976	7 days	7 days	0 days	16 days		3 weeks	Moe and Day (1979)
56°02'N 156°45'W	1976	1 day	0 days	0 days	16 days	24 days	17 days	Leschner and Burrell (1977)
56°47'N 156°41'W	1976	1 day	0 days	0 days	19 days	17 days	19 days	this study, Chapter I
	1977	6 days	6 days	1 day	18 days	17 days	23 days	this study, Chapter I
57° N 169°20'W							4-6 weeks	Preble and McAtee (1923)
58°55'N 153°10'W	1976	4 days	4 days	0 days	21 days	2-3 weeks	26 days	Amaral (1977)
	1977	7 days	7 days	0 days	15 days	1-2 weeks	23 days	Manuwal and Boersma (1978)
53°10'N 172°10'W	1966	c. 7 days	7 days		19 days		c. 3 weeks	Sealy (1973a)
	1967						"	
55°45'N 168°55'W		1 day				3 weeks	3 weeks	Kenyon and Brooks (1960)
60°08'N 166°08'W	1960	c. 7 days	0 days		19 days		2-4 weeks	Swartz (1966)
	1961						"	

Appendix II: Patterns of colony settlement during the pre-egg stage of Tufted and Horned puffins, Rhinoceros Auklets, and Common Puffins throughout their ranges.

Location	Coordinates	Year	Interval between arrival and first land-coming	Interval between arrival and continuous occupancy	Interval between first land-coming and continuous occupancy	Interval between continuous occupancy and start of egg-laying	Interval between first land-coming and start of egg-laying	Interval between arrival and start of egg-laying	Source
TUFTED PUFFIN									
Farallone Is., CA	37°40'N 123°00'W							c. 2 months	Grinne
Uruppu I., USSR	46°00'N 151°00'E			30 days		c. 0 days		4-6 weeks	Kozlov
Destruction I., WA	47°40'N 124°24'W	1974	7 days	30 days	24 days	1 week	c. 4 weeks	5-6 weeks	Frazer
Buldir I., AK	52°21'N 176°56'E	1975	6 days	14 days	38 days		13 days	19 days	this st
Attu I., AK	53°08'N 173°18'E	1974	9 days						J. L.
East Kamchatka, USSR	55° N 160° E		c. 10 days						Dement
Bering I., USSR	55°20'N 166°00'E							c. 6 weeks	Stejneg
Shumagin Is., AK	55°22'N 159°20'W	1976						19 days	Moe an
Nelson Lagoon, AK	56°00'N 161°10'W							3 weeks	R. Gill
Ugaiushak I., AK	56°47'N 151°41'W	1976		24 days	24 days	0 or 1 days	25 days	25 days	this st
		1977	0 days	26 days	26 days	0 days	25 days	25 days	this st
Pribilof Is., AK	57° N 169°20'W							c. 1 month	Preble
Barren Is., AK	58°55'N 152°10'W	1976	7 days	6 days	0 days	8 days	9 days	2 weeks	Amaral
		1977						8 days	Manuwa
St. Lawrence I., AK	63°10'N 172°12'W		c. 7 days					c. 3 weeks	Sealy (
Little Diomede I., AK	65°10'N 176°12'W		18 days						Kenyon
HORNED PUFFIN									
Buldir I., AK	52°21'N 175°56'E	1975	8 days	8 days	2 days	11 days	13 days	19 days	this st
Attu I., AK	53°05'N 173°18'E	1974	0 days						J. L.
Shumagin Is., AK	55°22'N 159°20'W	1976	7 days	7 days	0 days	16 days		3 weeks	Moe an
Chowiet I., AK	56°02'N 156°45'W	1976	1 day	0 days	0 days	16 days	24 days	17 days	Leschn
Ugaiushak I., AK	56°47'N 156°41'W	1976	1 day	0 days	0 days	19 days	17 days	19 days	this st
		1977	6 days	6 days	1 day	18 days	17 days	23 days	this st
Pribilof Is., AK	57° N 169°20'W							4-6 weeks	Preble
Barren Is., AK	58°55'N 153°10'W	1976	4 days	4 days	0 days	21 days	2-3 weeks	26 days	Amaral
		1977	7 days	7 days	0 days	15 days	1-2 weeks	23 days	Manuwa
St. Lawrence I., AK	63°10'N 172°10'W	1966	c. 7 days	7 days		19 days		c. 3 weeks	Sealy (
		1967							"
Little Diomede I., AK	65°45'N 168°55'W		1 day				3 weeks	3 weeks	Kenyon
Cape Thompson, AK	68°08'N 166°00'W	1960	c. 7 days	0 days		19 days		2-4 weeks	Swartz
		1961							"

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Coordinates	Year	Interval between arrival and first land-coming	Interval between arrival and continuous occupancy	Interval between first land-coming and continuous occupancy	Interval between continuous occupancy and start of egg-laying	Interval between first land-coming and start of egg-laying	Interval between arrival and start of egg-laying	Source
46°14'N 141°12'E							4-6 weeks	Kozlova (1957)
47°40'N 124°24'W	1974						1 month	Leschner (1976)
	1975						"	
40°08'N 122°55'W	1975						4-6 weeks	Wilson (1977)
	1976						"	
54°48'N 133°31'W	1913						4-6 weeks	Heath (1915)
44°30'N 67°06'W		8 days						Graham and Graham (1971)
47°11'N 52°46'W		5 days	30 days	26 days	0 days	2-3 weeks	c. 1 month	Nettleship (1972)
51°12'N 04°50'W		4-5 days	c. 40 days	c. 1 month	0 days	c. 4 weeks	4-6 weeks	Perry (1940)
51°42'N 05°16'W		6-14 days	27 days	4-5 weeks	0 days	c. 3 weeks	c. 1 month	Lockley (1934)
51°44'N 05119'W		1-2 weeks	c. 30 days	1-2 weeks	0 days	3-4 weeks	4-6 weeks	Ashcroft (1976)
56°12'N 01°32'W		2-3 weeks	c. 30 days	2-4 weeks	0 days	2-3 weeks	4-6 weeks	M. P. Harris (pers. comm.)
59°01'N 02°08'W		1-2 weeks					c. 1 month	Perry (1948)
65°12'N 19°45'W							6-8 weeks	Kartashev (1960)
66°20'N 12°20'E							35-38 days	Myrberget (1959, 1962)
68° N 35° E					0-14 days		4-6 weeks	Kozlova (1957), Belopol'skii (1957)
68° N 37° E							c. 1 month	Belopol'skii (1957)
72° N 54°46'E							c. 6 weeks	Uspenski (1958)
74° N 40° W							c. 1 month	Salomonsen (1950)

Appendix II. Continued

Location	Coordinates	Year	Interval between arrival and first land-coming	Interval between arrival and continuous occupancy	Interval between first land-coming and continuous occupancy	Interval between continuous occupancy and start of egg-laying	Interval between first land-coming and start of egg-laying.	Interval between arrival and start of egg-laying	Source
RHINOCEROS AUKLETS									
Moneron I., USSR	46°14'N 141°12'E							4-6 weeks	Kozlova
Destruction I., WA	47°40'N 124°24'W	1974						1 month	Leschne
		1975						"	
Protection I., WA	48°08'N 122°55'W	1975						4-6 weeks	Wilson (
		1976						"	
Forreuter I., AK	54°48'N 133°31'W	1913						4-6 weeks	Heath (
COMMON PUFFIN									
Machias Seal I., ME	44°30'N 67°06'W		8 days						Graham
Great I., Newfoundland	47°11'N 52°46'W		5 days	30 days	26 days	0 days	2-3 weeks	c. 1 month	Nettlesh
Lundy I., U.K.	51°12'N 04°50'W		4-5 days	c. 40 days	c. 1 month	0 days	c. 4 weeks	4-6 weeks	Perry (
Skokholm, U.K.	51°42'N 65°16'W		6-14 days	27 days	4-5 weeks	0 days	c. 3 weeks	c. 1 month	Lockley
Skomer I., U.K.	51°44'N 05119'W		1-2 weeks	c. 30 days	1-2 weeks	0 days	3-4 weeks	4-6 weeks	Ashcrof
Isle of May, U.K.	56°12'N 01°32'W		2-3 weeks	c. 30 days	2-4 weeks	0 days	2-3 weeks	4-6 weeks	M. P. I
Orkney I., U.K.	59°01'N 02°08'W		1-2 weeks					c. 1 month	Perry (
Iceland	65°12'N 19°45'W							6-8 weeks	Kartash
Lovunden, Norway	66°20'N 12°20'E							35-38 days	Myrberg
Seven Is. USSR	68° N 35° E					0-14 days		4-6 weeks	Kozlova
East Murman, USSR	68° N 37° E							c. 1 month	Belopol'
Novaya Zemlya, USSR	72° N 51°46'E							c. 6 weeks	Uspensk
Greenland	74° N 40° W							c. 1 month	Salomon